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On the Physics & Physiology of Protoplasmic Streaming in Plants

By Alfred J. Ewart, D.Sc., Ph.D., F.L.S.

Lecturer on Botany in the Birmingham Technical Institute

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Francis Gotch, D.Sc. (Oxon.), F.R.S.

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PREFACE

THE following work is the outcome of a series of observations commenced at Leipzig in 1894, continued in Birmingham 1897–1898, and during a two years' stay in Oxford (1898–1899), but not completed until 1902 in Birmingham. For convenience, the Physics (including Chemistry) and the Physiology of protoplasmic movement are arranged in separate chapters, although any such division is entirely arbitrary. Under the first heading those phenomena of protoplasmic movement are discussed which can be directly referred to physical and chemical causes, whereas under 'Physiology' we deal with those 'vital' phenomena which cannot as yet be thus resolved. The work on which the latter chapter is based was mainly carried out at Oxford, but almost all the purely physical work has been done in Birmingham, and a part of the latter could not have been accomplished had not Prof. Poynting kindly placed the resources of the Physical Department of Birmingham University at my disposal. I must also record my indebtedness to Prof. Vines, Prof. Gotch, and Sir Oliver J. Lodge, for various suggestions and criticisms.

An abstract of this paper was read to the Royal Society in February of the present year, and it is owing to the generous financial aid accorded by the Society that I am able to publish this work as a separate treatise.

BIRMINGHAM, *December*, 1902.

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CHAPTER I

INTRODUCTION

SECTION 1. **Historical.**

AT a very early date the attention of scientific observers was drawn to the streaming movement exhibited by the cell-contents of many plants. Thus Corti[1] in 1774 pointed out that the fluid contents of certain aquatic plants and also of some terrestrial ones (*Cucurbita*, *Mercurialis*, *Solanum*, &c.), in all about thirty species, frequently exhibited streaming movements. These observations were confirmed by Fontana, but at the time the existence and character of protoplasm, the basis of all life, was still unknown, and Corti apparently concluded that what he observed was simply a movement of the cell-sap, although he noticed that it ceased after the cells had been immersed for some hours in olive oil, and that it became slow at low temperatures, more rapid at high ones.

These forgotten observations were revived by Treviranus in 1807[2]. At a later date Amici[3] studied rotation in *Chara* and considered it to be an electrical phenomenon, the chloroplastids acting as the motor-mechanism. Streaming was also observed by the Englishman Slack[4] in *Nitella flexilis* and *Hydrocharis Morsus-ranae*, and by Meyen[5] in *Vallisneria*, *Stratiotes*, *Potamogeton*, and in the root-hairs of several terrestrial plants. Even before this R. Brown had observed streaming in the staminal hairs of *Tradescantia*. Slack's figures are remarkably accurate, 'protoplasm' nucleus, cell-sap, direction of streaming, indifferent lines, threads, &c., all being shown, but neither this observer nor even Dutrochet recognized

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[1] Osservazioni microscopiche sulla Tremella e sulla circolazione del fluido in una pianta acquaiula, Lucca, 1774, p. 127.

[2] Physiologie, 1807.

[3] Mem. della Soc. Ital. delle Scienze in Modena, XVIII, p. 182, 1818.

[4] Ann. sci. nat., 1834, ii. sér., T. I, pp. 193, 271.

[5] Ann. sci. nat., 1835, ii. sér., T. IV, p. 257.

that the protoplasm was the living part of the cell, and the seat of active movement. Dutrochet[1] observed the influence of acids, alkalies, alkaloids, saline and sugary solutions, temperature, light, oxygen and mechanical stimuli on streaming in *Chara fragilis*, while the influence of electrical stimuli was investigated by Dutrochet and Becquerel (loc. cit., p. 80). These empirical studies form the basis of our present knowledge of the influence of stimuli on streaming movements, and though elementary in scope are extremely exact. Schleiden[2] and Hassal[3] observed that rotation is not confined to the cell-sap, but is most obvious in the outer denser granular layers (of endoplasm) or in the 'mucus' bridles crossing the cell. It was not, however, until Von Mohl had established the fact that the protoplasm forms the essential living substance of all plant (and animal) cells that Schacht[4] showed the seat of the active movement to be in the protoplasm, and concluded that it was merely an outward and visible sign of the vital activity of the latter. Von Mohl studied the same phenomenon, and determined the velocity of streaming between 15° and 16° R. in a variety of plants[5]. He concluded that the nucleus exercised little or no influence, and that the chloroplastids played a directly active part in inducing streaming, but gave up this view later[6].

Nägeli[7] in 1860 investigated more exactly the relation between streaming and temperature, and showed that a geometric proportionality existed between the increments of temperature and of velocity. Both Nägeli and Pringsheim[8] held that the force inducing movement had its origin between the cell-sap and the lining layer of protoplasm, a theory which Berthold still upholds, but one to which considerable doubt attaches.

Kühne established the necessity of a supply of oxygen for the movement, and indeed concluded that contact with oxygen formed the necessary essential stimulus to protoplasmic movements of all kinds[9].

My own observations, however, showed that streaming might continue in certain cases for prolonged periods of time in the absence of oxygen, and these observations have subsequently been confirmed by Kühne himself, and in part also by Ritter[10].

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[1] Ann. sci. nat., 1838, ii. sér., T. IX, pp. 5, 65.

[2] Principles of Botany (Eng. Trans.), 1849, p. 92.

[3] British Freshwater Algae, I, p. 85.

[4] Die Pflanzenzelle, 1852, p. 340.

[5] Von Mohl, Bot. Zeitg., 1846, p. 73.

[6] Vegetable Cell, 1852, p. 39 (Eng. ed.).

[7] Beiträge zur wiss. Botanik, 1860, II, p. 62.

[8] Nägeli u. Schwendener, Das Mikroscop, p. 399; Pringsheim, Unters. über den Bau und die Bildung der Pflanzenzelle, Berlin, 1854, p. 9.

[9] Kühne, Unters. über das Protoplasma und die Contractilität, 1864, p. 105.

[10] Ewart, On Assim. Inhib., Journ. Linn. Soc., 1895, Vol. XXXI, p. 42; N. Kühne, Zeitschr. f. Biol., 1897, Bd. XXXV, pp. 43-67; 1898, Bd. XXXVI, pp. 1-98; G. Ritter, Flora, 1899, LXXXVI, pp. 329-60.

With regard to the importance of the movements of the protoplasm in closed cells, various contradictory opinions have been expressed. Velten[1] held that rotation was a very common phenomenon, and was exhibited by the protoplasm of all cells at some stage or other of their life-history. It does not, however, follow that the power of movement must always take this particular form, or be immediately perceptible. Slow movements and changes of form of the protoplast and its organs seem, however, to be possible in all cases where no insurmountable physical obstacles are interposed. De Vries[2] considered that streaming movements were of primary importance for the transport of food-materials and even of water, and held that so long as any cell could generate energy its protoplasm was in active movement. This one-sided view was supported by Janse[3], who observed that in *Caulerpa prolifera* currents flow to and from the growing apices, and that after wounding they usually make a detour to reach their original destination, which otherwise dies. In those cases where no streaming could be detected, de Vries supposed either that it was too slow to be visible, or that the act of preparation had caused it to cease. Frank[4] showed, however, that in most cases there is no active movement, but that an external influence (section-cutting, change of temperature, &c.) can bring streaming into play, and that this may cease again after a time, or may persist during the remainder of the cell's existence. A particular stimulus is not always effective. Thus Moore[5] found that leaves of *Elodea* might be sectionized without streaming ensuing, and indeed no stimulus can induce streaming unless the protoplasm has an inherent tendency to that form of activity, and unless the necessary physical conditions are fulfilled.

Ida A. Keller[6] stated that streaming was in most cases not a normal phenomenon in the life of the cell, but was induced by injury or external stimulation, and that whenever normal streaming was present in a cell external stimuli simply increased its rapidity and intensity. Neither of these statements, however, applies to all cases, and the exceptions to the latter one are especially numerous. Wigand[7] supposed that long resting-periods alternated with short periods of active rotation, and concluded that streaming was awakened in cells under observation not so much by the mechanical influence of preparation, as by the reflected light and heat rays to which the preparation is subjected on the microscope-stage. Hauptfleisch[8], however, has shown that a mechanical stimulus alone is sufficient to

[1] Bot. Zeitg., 1872, p. 147; Flora, 1873, p. 82.
[2] Ueber die Bedeutung, &c., Bot. Zeitg., 1885, Nos. 1 and 2, p. 1.
[3] Jahrb. f. wiss. Bot., 1890, Bd. XXI, p. 163.
[4] Pringsh. Jahrb., 1872, VIII, p. 220.
[5] Journ. Linn. Soc., 1888, Vol. XXIV, p. 240.
[6] Ueber Protoplasmaströmung im Pflanzenreich, 1890, pp. 12, 40.
[7] Botanische Hefte, 1885, I, p. 214; cf. also Hanstein, Das Protoplasma, 1880, p. 169.
[8] Pringsh. Jahrb. f. wiss. Bot., 1892, Bd. XXIV.

induce streaming, which is then independent of the action of light. The same author distinguishes between the primary streaming which occurs as a normal phenomenon in certain plants or parts of plants, and the secondary streaming produced by mechanical, chemical, or physical stimuli in previously quiescent cells. These distinctions are purely artificial ones, for in certain cases the 'primary' streaming may cease, and yet the cell may remain capable of exhibiting 'secondary' streaming when stimulated. Hauptfleisch also erroneously states that mechanical stimuli, if they do not cause death, do not stop streaming, whereas as we shall see later a temporary stoppage is readily induced by various mechanical stimuli which produce no permanently injurious effect.

As regards the influence of external agencies upon streaming a very large amount of work has been done, the results of which are in many cases contradictory. This is especially the case in respect to the action of carbon dioxide, oxygen, and other gases, the discordant results obtained by different investigators being in certain cases due to specific differences between the physiological properties of the plants employed, and in other cases being due to experimental errors or the use of impure gases [1].

Concerning the physics of streaming movements little is known, nor has any attempt been made to determine even approximately the amount of work done by the streaming protoplasm of a closed cell in overcoming the friction and cohesion between its rotating and stationary layers. If the amount of energy expended could be directly estimated it would be easy to find relative values for the other factors in the equation, but unfortunately the energy produced by respiration is never wholly employed in the production of movement. The difficulties in the way of direct experimental research are therefore very great, but by various methods which will be described later it is possible to obtain approximate estimations of the forces at work and the resistance offered to their action.

It is only in very few cases that streaming persists during the entire existence of the adult cell, and that it is so closely connected with the vitality of the latter that permanent cessation always indicates a fatal injury (*Chara*, *Nitella*, and the cells of a few Phanerogams). In most cases streaming is a more or less transitory phenomenon, and is frequently induced by external stimuli, chemical, physical, or mechanical. Thus when a leaf of *Elodea* is torn off, after a short latent period streaming appears at the base of the leaf near the point of injury, and later in successive regions spreading away from it. Now Richards [2] has shown that when

[1] The literature will be given in detail subsequently. On carbon dioxide cf. Kabsch, Bot. Zeitg., 1862, p. 340; Stich, Flora, 1891, XLIX, p. i; Frankel, Zeitschr. f. Hygiene, 1889, Bd. V, p. 332; Arsonval, Compt. rend., 1891, T. CXII, p. 667.

[2] Ann. of Bot., 1896, Vol. X, p. 531.

a plant is injured, respiration becomes after a time more active near the wounded area, and at the same time a slight rise of temperature occurs. This effect also slowly radiates a slight distance from the injury, but the appearance of streaming precedes the maximum increase in respiratory activity, and therefore simply heralds and perhaps aids in the subsequent marked increase of katabolism instead of being caused by it. Streaming does not always ensue as the result of injury, and hence its occasional appearance is more probably due to a diminution in the resistance to flow permitting a pre-existent tendency to streaming to become externally manifest, than to an actual induction of this tendency as the result of injury.

The conditions determining the flow of liquids through capillary tubes were first investigated by Poiseuille [1], who established a formula expressing the relationship of these conditions and also endeavoured to trace the influence of different dissolved substances upon the movement of the blood in the blood-capillaries. In the case of plant-cells, however, the flow is in closed tubes, and takes place in opposite directions on the two sides of the capillary, none of the moving fluid escaping from either end (cf. Fig. 5, p. 28).

[1] Mém. des Sav. Étrang., 1846, IX, p. 433.

CHAPTER II

PHYSICS OF STREAMING

SECTION 2. Mechanics and Mechanical Models.

THE first of the physical problems connected with protoplasmic streaming which require solution are: (1) the source or sources of energy, (2) the character and mode of application of the force or forces inducing movement, (3) the amount of work done in overcoming resistance. The first two of these questions can only be answered in general terms, but the third can readily be solved with approximate accuracy by indirect experiment. It will tend to a clearer understanding of the problems at issue if we first consider them in simplified form in relation to a mechanical model.

If a cylinder of water is placed vertically, and one side heated while the other is cooled, the convection currents set up will assume a regular direction around the long axis of the cell. This was first used as an illustration by Dutrochet [1], but it is an imperfect one, for the current can never be mainly horizontal, as it may be in elongated living cells. A better model is formed by a metal box, filled with cold water, and having a number of obliquely inserted tubes closed at their outer ends inserted in its walls (Fig. 1). The outer ends of the tubes are strongly heated, and the escaping steam imparts by intermittent impulses an onward movement to the surrounding water before it is entirely condensed again. By using tubes of fairly large bore, and inclining them slightly downwards, they may be kept filled with water without any appreciable backward flow being set up. When in action the outer layers of water will be at rest, further inwards the velocity steadily increases to a maximum, then falling again to *nil* at the centre of the cell. The wall of the box corresponds to the cell-wall, the outer stationary layers to the ectoplasm, the inner rapidly moving layers to the endoplasm, while the central portion, which is moved by friction against the layers outside it, corresponds to the cell-sap, whose motion appears to be passively induced.

If the box were closed, provided with a safety-valve and placed in an erect position, the force of gravity would counterbalance on the two

[1] Ann. sci. nat., 1838, ii. sér., T. IX, p. 24.

sides, so that the same amount of energy would be expended as before in imparting to the moving fluid the same average velocity. In the case of living cells, however, a physiological response to gravity might be made, and more or less energy be liberated on the side where the stream ascends than on that where it descends (Sect. 9).

The mechanical model suffices to show that, given materials of definite structure, motion may be set up in a fluid by interaction with a non-moving layer which it touches and which by friction reduces the velocity of the layers immediately touching it to *nil*. When the average internal velocity is constant, the total work done by the expanding steam must just counterbalance the total work done against friction by the moving layers. These exert a shearing strain upon the outer rigid wall tending to drag it round with them, and under theoretical conditions this forwardly directed force will be just counterbalanced by the backward reaction of the expanding steam. Hence when freely suspended, the model as a whole should remain at rest with regard to surrounding objects, and the same should be the case when the velocity is decreasing, for the propelling force, and hence the equal and opposite backward reaction, can never be less than the force due to friction. When, however, the velocity is increasing, the propelling force and its backward reaction are greater than the force due to internal friction, hence the model when freely suspended will spin round as a whole in the opposite direction to that of the internal current. As a matter of fact this is always the case, partly because the average internal velocity is never constant, and partly because there is a certain amount of lateral friction and displacement.

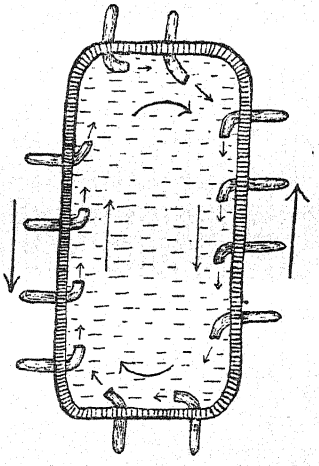

FIG. 1. Mechanical model of rotating cell. The arrows show the direction of movement.

If short, living cells of *Chara* and *Nitella*, in which the direction of streaming is nearly parallel to the long axis of the cell and on opposite sides of it, are suspended in still, moist air by single fibres of unspun silk, they soon come to rest, but the fibre, when viewed through a horizontal microscope, exhibits no distinct torsion to one side or the other. A mechanical stimulus sufficient to cause a temporary cessation of streaming, lasting until the swinging vibrations have ceased, can readily be applied to cells suspended in this manner. A slight tremor can often be observed when streaming recommences. Occasionally a slight but distinct swing occurred, followed by one in the opposite direction caused by the torsion in the fibre. On examination the first swing was seen to be in the

opposite direction to that of streaming, but the phenomenon may not be directly connected with the reappearance of streaming, since it might be caused by localized changes of surface-tension, by the diosmosis of liquid, or by a displacement of the centre of gravity due to localized contractions or change of shape.

It becomes a question of considerable interest as to what effect will be produced by removing the supporting cell-wall from the ectoplasm of a cell exhibiting rotation, and by separating the protoplasmic contents into two or more distinct masses. If strong induction shocks are passed through a cell, the protoplasm often separates into a number of balls, in which streaming may recommence, lasting either until they reunite or ceasing again if the cell ultimately dies. Velten[1] states that the periphery of such balls is always at rest, but this might be due to their bases adhering to the cell-wall beneath them. That this is so can easily be shown by inclining the preparations and noting that they usually retain their original positions although denser than the cell-sap.

If, however, fragmentation is induced by immersal in a plasmolyzing solution (3 to 5 per cent. KNO_3, 15 to 25 per cent. $C_{12}H_{22}O_{11}$, 8 to 12 per cent. $C_6H_{10}O_5$) which is subsequently slightly diluted, or if cells are opened in an isosmotic solution of sugar, balls of plasma are sometimes obtained which float freely and may exhibit streaming for hours[2], but the ball as a whole exhibits no tendency to roll round in the opposite direction to that of streaming, even when streaming is active. On more than one occasion, however, spheres exhibiting streaming during or shortly after their formation remained temporarily connected to the main mass of plasma by a protoplasmic thread, which was drawn out until it broke in such a fashion as though the ball as a whole was slowly rotating in the same direction as that of streaming (Fig. 2). In another case, however, the reverse was the case, so that this peculiar phenomenon may be safely ascribed to causes unconnected with the internal streaming movements.

If only partial plasmolysis is produced, the velocity of streaming in regions where the ectoplasm is free can be compared with that in regions where it is still adherent to the cell-wall. Chloroplastids floating in the peripheral endoplasm are often distinctly retarded at such points as at A, Fig. 3, and may be caught up by those behind them. This may, however, be simply due to the inward bulging at A, producing a tendency to eddy currents and hence causing a loss of momentum. When crossing the curved region, a chloroplastid may often be seen, if floating near to the internal limit of the endoplasm, to have a slight aggregation of protoplasm

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[1] Flora, 1873, p. 101.

[2] *Chara* and *Nitella* are unsuitable. Cells of *Elodea*, *Vallisneria*, *Aristolochia*, *Sagittaria*, as well as hairs of *Trianea* and *Cucurbita* may be used. For methods of determining isosmotic values cf. Pfeffer's Physiol. Vol. I (Clar. Press), p. 145.

around it, which drags out behind like a tail. At first this looks as if the chloroplastid had an active power of movement of its own, but the explanation probably lies in the greater momentum of the chloroplastid, or in the fact that in a fluid flowing around a curve the velocity is greater on the convex side than on the concave one which is the shorter path, the internal friction being thereby reduced to a minimum. At the point B, the path of the current is shortened, at A it is lengthened, and in the latter case, owing to the shape of the curvature, the pressure due to surface-tension is added to the internal osmotic pressure instead of acting against it. The finer floating particles have a slightly greater velocity at B than at A, that at B being slightly above, and that at A slightly below the mean over the rest of the cell. If, however, the ectoplasm is only just separated from the cell-wall no such differences are perceptible. Hence the mere separation of the cell-wall and protoplasm does not in itself retard the velocity of streaming, and direct contact between the ectoplasm and cell-wall is not necessary for the maintenance of rotation. No movement is shown in ectoplasmic layers unsupported by a cell-wall, nor is any translatory movement perceptible in the liquid lying between the ectoplasm and cell-wall.

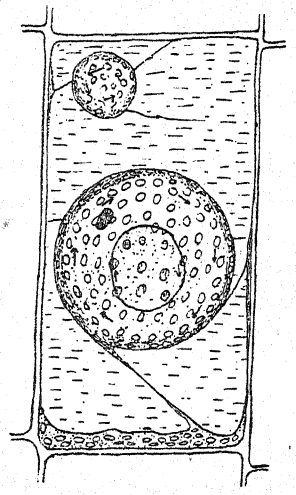

FIG. 2. Streaming cell of *Elodea* fragmented by plasmolysis. The largest thread on each ball has just broken.

O. Müller[1] has shown that the forward movements of certain diatoms are due to the presence of peripheral strands of plasma streaming in the opposite direction, and returning by a central path in the body of the diatom. The friction of these bands against the water causes the diatom as a whole to move in the opposite direction, and Müller has calculated that in *Nitzschia sigmoidea* the rapidity of streaming in the external protoplasmic bands must be approximately 50 μ per sec. to give the forward velocity of 17 μ per sec. usually shown by this form. We are, however, here dealing with an exceptional condition of things, for in ordinary plant cells covered by cell-walls no such direct interaction with an external medium is possible.

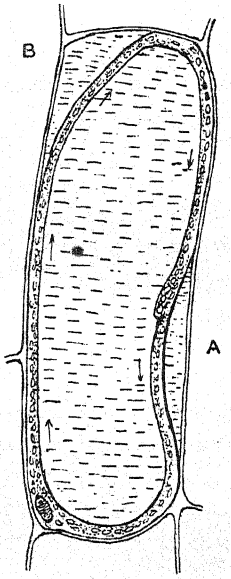

FIG. 3. Partially plasmolyzed streaming cell.

[1] Ber. d. D. Bot. Ges., 1896, Bd. XIV, p. 117.

SECTION 3. The Influence of Osmotic Pressure, Percentage of Water, and of Viscosity on Streaming.

These three factors are all closely connected with one another. Thus the removal of water from the cell increases the osmotic pressure of the cell-sap, and also the viscosity of the protoplasm. A rise of osmotic pressure caused by an increase in the percentage of salts in the cell-sap will force the protoplasmic micellae closer together and squeeze out some of its water of imbibition, thus increasing its viscosity and resistance to flow. A decrease in the concentration of the cell-sap will permit the protoplasm to imbibe more water, and hence will, *ceteris paribus*, decrease the viscosity and increase the velocity of streaming.

Osmotic pressure. Kohl[1] observed that the immersal of streaming cells of *Elodea* and *Tradescantia* in weak solutions of asparagin was followed by an increase in the rapidity of streaming, and considered this to be due to the fact that the solution diminishes the pressure of the cell-sap against the protoplasm and cell-wall, and hence decreases the friction between these two. The suggestion is even made that changes in the internal osmotic pressure may be the causes directly determining the cessation or commencement of streaming. Strong solutions always retard rotation, and the accelerating action of dilute solutions is not confined to asparagin, but may be produced by a variety of substances such as KNO_3 (·5 to 1 per cent.), cane sugar (5 per cent.), grape sugar (2 to 3 per cent.), and even glycerine. Similarly, streaming may be caused to appear in the cells of sections cut from seedlings of *Brassica* and *Sinapis* by immersing them in ·5 per cent. KNO_3 for a few hours and then placing them in water. It is usually the case that the most active streaming is shown on returning the cells to water, and frequently it is not until this has been done that the velocity increases. Again, dilute glycerine rapidly penetrates most protoplasts, and hence cannot maintain any permanent plasmolytic action, but nevertheless it may exercise the same effect as the other substances mentioned in inducing and accelerating streaming. Dilute solutions of KNO_3 (·5 to 1 per cent.) retard streaming very markedly in certain cases[2] (*Chara*, *Nitella*, *Spirogyra*), and ·2 to ·5 per cent. solutions of sodium chloride exercise a similar action. Even more dilute solutions may produce similar effects after prolonged immersal. Here, and in other cases also, there is no immediate connexion between the action of the solution and its osmotic concentration. Hence the action in question is undoubtedly an obscure stimulating one, and differs in character according to the substance

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[1] Bot. Centralbl., 1898, Bd. LXXIII, No. 5, p. 168.

[2] This is partly, though not entirely, the result of the low internal osmotic pressure in these plants.

used and the plant examined. Kohl is therefore incorrect in supposing the increased velocity to be due to a diminution of the pressure of the cell-sap against the lining layer of protoplasm. As a matter of fact the internal pressure does not decrease, but *increases* by an amount corresponding to the osmotic concentration of the external solution, and the external friction takes place between the rotating layers and the outer non-moving layers of ectoplasm, not between the latter and the cell-wall.

Fluid friction differs markedly from solid friction in one important respect. Thus the flow of an *incompressible* liquid through a tube of uniform bore with smooth walls depends solely on its viscosity, upon the diameter of the tube, and upon the difference of pressure at its two ends, but is not influenced by the lateral pressure on the containing walls. Thus pressures at the two ends corresponding to 0 cm. and 20 cm. of mercury respectively will produce the same rate of flow as pressures of 200 and 220 cm. respectively.

Protoplasm, like other substances capable of imbibition, contains, however, a large quantity of water which can be driven from it by pressure[1]. As the percentage of imbibed water decreases, the pressure required to squeeze out more water increases very greatly.

Now the pressure of the cell-sap on the protoplasm varies from 10 to 25 atmospheres in ordinary turgid cells, and its percentage of water is usually about 70. Hence a rise of at least 3 to 6 atmospheres (1 to 2 per cent. KNO_3) in the osmotic pressure would be necessary to squeeze out any appreciable quantity of water from it, even supposing it held no osmotic substances in solution, and exerted no appreciable osmotic pressure itself. Any withdrawal of water, however, increases the viscosity, hence, *ceteris paribus*, diminishing the velocity of streaming. It follows, therefore, that whenever a solution whose osmotic concentration is less than 1 per cent. KNO_3 markedly retards (or accelerates) streaming, even when the shock of sudden immersal is avoided by a gradual increase of concentration, it does so, not necessarily because of any osmotic action, but probably because the substance in question acts as a chemical stimulus. Dilute salt solution acts very largely in this way on cells of *Chara* and *Nitella*, but in most cases its action is mainly physical, and hence fairly strong solutions are necessary to produce a pronounced effect. Similarly whenever a very dilute solution causes a gradual decrease in the velocity of streaming, its action is that of a retarding chemical stimulus.

A rise of temperature of 15° C. causes an increase of 5 per cent. in the osmotic pressure of the cell-sap, but will not perceptibly affect the percentage of water in the protoplasm, even when it contains very much imbibed water and its inherent osmotic pressure is low. On the other

[1] Cf. Reinke, Nachr. d. Ges. d. Wiss. zu Göttingen, 1894, p. 54.

hand the direct action of a rise of temperature is to increase the respiratory activity, and to decrease the viscosity of the moving fluids; both of which factors are more powerful ones than the indirect action of the increased osmotic pressure.

SECTION 4. Percentage of Water.

Velten, and subsequently Hauptfleisch[1], concluded that there is a certain optimal percentage of water, varying in different objects, at which streaming is most active. Embryonic cells containing relatively little water show no streaming, which commences as they grow older, becomes active circulation when vacuoles appear, and turns into rotation when a single large central vacuole is formed. The presence of a vacuole, however, simply shows that the percentage of water in the cell increases, and says nothing as to the percentage present in the protoplasm, which is the really important point. The latter is dependent upon the osmotic pressure of the cell-sap, the force of imbibition, and upon the amount and character of the soluble osmotic materials present in the protoplasm.

Little is known as to the relative percentages of water in the protoplasm of young solid cells, and of older vacuolated ones. In the former case the osmotic pressure of the protoplasm and of the entire cell are the same. During active growth this pressure can never be considerable, since the consumption of food materials is rapid, and the cell-wall thin and extensible. The latter appears in fact usually to lie between 3 to 6 atmospheres, which is about the minimum osmotic pressure (3 to 5 atms.) to which adult phanerogamic cells can be reduced by starvation. The values obtained by applying plasmolytic solutions to growing apices or apical cells are frequently much higher than the true ones, since the highly extensible cell-walls of such cells may collapse to a considerable extent before the protoplasm shrinks away from them. Indeed, in certain cases, the cells cannot be plasmolyzed at all[2]. If, however, the osmotic concentration is observed at which the cell begins to decrease in size, this gives its true osmotic pressure. Actively growing root apices, the meristems of seedlings, the apical cells of *Selaginella* and ferns, gave approximately the values already mentioned, but any retardation of growth is rapidly followed by a rise of osmotic pressure at the growing points if the plant is well nourished. If solutions of glycerine are applied to apices of *Selaginella*, they must be fairly strong to produce any distinct retraction. Thus a 10 per cent. solution may produce no retraction, although its osmotic pressure is 30 atmospheres, and 10 to 20 per cent. solutions which cause distinct plasmolysis of the uncuticularized cells behind the apex may not

[1] Velten, Bot. Zeitg., 1872; Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 213.
[2] Cf. Pfeffer, Druck- u. Arbeitsleistungen, 1893, p. 307.

affect the apical cells. When dilute solutions are suddenly applied, however, the cases may be reversed. This is obviously due to the apical cells being more readily permeable by glycerine than the older cells derived from them.

It seems, therefore, that the protoplasm of the embryonic cells at actively growing apices is relatively rich in water, and if the force with which the protoplasm imbibes water remains the same, or nearly the same in adult cells, it must on the whole contain less water than that of very young cells. The statement, therefore, that active rotation appears in adult cells because their percentage of water increases, indicates not a causal but an accidental relationship, and moreover, as far as the evidence goes, the osmotic pressure rises and the percentage of water in the protoplasm decreases slightly as the cell becomes adult. It is also certain that the protoplasm can increase and decrease its own viscosity independently of its percentage of water[1], and probably such changes are often the chief or even the sole factor in determining the appearance or the cessation of streaming in particular cases. There are, however, two instances in which an increased percentage of water in the protoplasm is of primary importance. Firstly, when cells in which streaming has ceased owing to immersal in strongly plasmolytic solutions are returned to dilute solutions, so that the protoplasm can re-imbibe the water withdrawn from it and recommence streaming. Secondly, when streaming appears, as is often the case, in cells from which large stores of soluble reserve materials are being removed. In both cases, however, other factors, such as changes in the respiratory activity, &c., may come into play.

Hauptfleisch considers the absence of streaming from so many adult cells to be due to the presence of an infra-minimal or supra-maximal percentage of water in them. Many of the instances quoted by Hauptfleisch (l. c., p. 213), however, bear a different interpretation to that which he gives. For example, rotation appears over an area of a leaf of *Vallisneria* or *Elodea* exposed to air, not because the percentage of water in the protoplasm has fallen to the optimal amount for streaming, but because the loss of water acts as a stimulus, which is propagated to neighbouring cells in which the percentage of water is unaltered. Similarly when dilute solutions of salt, glycerine, or asparagin induce or accelerate streaming, they do so, not owing to any decrease in the percentage of water in the protoplasm, but because they exercise an indirect stimulating action. The latter is shown by the fact that the velocity usually undergoes a further increase on returning to water, and that streaming will appear if the cells are removed from the solution and replaced in water before it has actually commenced.

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[1] See Pfeffer's Physiology, 1900, Vol. I, p. 45, Eng. ed.

That the presence of a certain percentage of water varying within wide limits is an essential condition for streaming is certain, but this is neither the cause of streaming nor an explanation of it. The percentage of water not only affects the viscosity of the protoplasm and the osmotic pressure of the cell-sap, but may also modify the respiratory activity and amount of chemical change occurring in the cell, in virtue of the influence of relative mass, and hence of dilution and concentration upon chemical action. Bastit and Jumelle (Lichens and Mosses) and Aubert (Crassulaceae) [1] have shown that in the case of plants which can withstand partial or complete dessication, the activity of respiration steadily increases as the plants are allowed to imbibe water, although above a certain optimal limit further saturation with water causes a secondary decrease in the respiratory activity. Hence it is possible that in certain cases a decrease in the percentage of water might increase the supply of kinetic energy available for rotation, and that this might more than counterbalance the retarding effect of the concomitantly increased viscosity. These facts also suffice to show the inadequacy of Kohl's supposition that the vacuolar pressure determines the presence or absence of rotation, and that a diminution of the vacuolar pressure acts as a direct physical cause, like the removal of a brake, increasing the activity of streaming or rendering it possible.

The mechanical and physical effects produced by an osmotic solution must always be distinguished from its indirect stimulating action. The indirect acceleration of streaming which may be caused by the stimulating action of weak solutions of many substances is usually only temporary; but if after prolonged immersal the velocity becomes the same, or even less than it was at first, this is partly due to a direct physical action. Moderately strong osmotic solutions always decrease the activity of streaming, the direct physical action preponderating, but irregular variations may occur at first, and these are probably the result of some indirect stimulating action. Very strong plasmolytic solutions such as 8 to 10 per cent. KNO_3; 6 to 8 per cent. NaCl; 40 to 50 per cent. cane sugar, and 25 per cent. glucose always cause an immediate stoppage if suddenly applied, whereas if the concentration is gradually raised, streaming slowly and progressively decreases to nil. If the immersal has not been too prolonged, streaming may recommence in water, either after a short interval, or after one extending to several hours in some cases. That the effect produced is not due to the plasmolysis, but to the withdrawal of water from the protoplasm, is shown by placing streaming cells in solutions of glycerine of gradually increasing strength, when streaming is gradually retarded, and ultimately ceases without any plasmolysis being produced.

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[1] Bastit, Rev. gén. de Bot., 1891, T. III, p. 476; Aubert, ibid., 1892, T. I. IV, p. 379; Jumelle, ibid., 1892, T. IV, p. 169.

The leaf-cells of plants of *Elodea* kept in 10 to 20 per cent. sugar solutions for two to three months in darkness may still contain apparently normal and green chloroplastids, but show no streaming and no power of carbon dioxide assimilation. On reaccustoming to water the latter may slowly return in part, but not the former, whatever stimuli are applied. Apparently the protoplasm has been brought to such a condition of increased viscosity that streaming is no longer possible, but in new leaves formed by apical growth it can readily be induced.

SECTION 5. The Influence of Streaming on Osmotic Pressure and Diosmosis.

There is no perceptible change in the osmotic pressure or in the diosmotic properties as the result of the commencement of streaming in a previously quiescent cell (*Elodea*, *Vallisneria*, *Trianea Bogotensis*, *Aristolochia Sipho*, *Lepidium*, *Tradescantia*). The osmotic pressure was tested in the usual manner, and the diosmotic properties by immersal in very dilute solutions of various aniline dyes. Actively rotating cells often accumulate a dye, viz. methyl-blue, more rapidly than resting ones, but this may be due to the presence of an increased percentage of substances in the cell-sap, which cause the dye to be precipitated in a non-diosmosing form, viz. tannate of methyl-blue. By treatment with dilute acid the dye may be removed[1], and the observations may be repeated on cells which have ceased or which have commenced to rotate. Since an increase in the rapidity of absorption (as well as an occasional decrease) may be shown in both cases it is obviously unconnected with streaming, but is due to the treatment with acid (or to the alteration or escape of certain constituents of the cell-sap). Moreover, using methyl-violet and cyanin, which diosmose away again in pure water, no constant difference in the rate of absorption was perceptible between cells when rotating and when quiescent. The presence of rotation does, however, seem to be indirectly connected with a fall of the osmotic pressure in certain cases. Thus if leaves of *Elodea* are kept in well-aerated water in darkness for five to ten days at 25° C. the osmotic pressure in the rotating cells of a leaf may be less on the average by ·2 or even ·5 per cent. KNO_3, or 1·5 to 4 per cent. cane sugar, than it is in the quiescent cells[2]. This is probably due to the rotating cells consuming more food materials and hence reducing the percentage of soluble substances in the cell-sap, but it might also be the result of increased diosmosis. After more prolonged starvation all the cells fall to about the same average osmotic pressure, and no constant difference is perceptible between quiescent cells and ones which show, or have shown, rotation.

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[1] Pfeffer, Unters. a. d. Bot. Inst. zu Tübingen, 1886, Bd. II, p. 286.

[2] In individual cases the difference may amount to as much as 1 per cent. KNO_3.

SECTION 6. The Influence of the Viscosity of the Protoplasm and Cell-sap.

The viscosities of the protoplasm and of the cell-sap are factors of the utmost importance in dealing with protoplasmic movements in plant-cells, although little or no attention has hitherto been paid to them. The importance of this purely physical property is sufficiently indicated by the fact that the viscosity of water at 30° C. is one-half what it is at 0° C., while that of glycerine containing a little water is one-fifth at 20° C. of what it is at 3° C. This decrease of viscosity with rise of temperature is a general phenomenon, and seems almost sufficient to explain the acceleration of streaming produced by moderate rises of temperature, although, as we shall see subsequently, the causation of the increased velocity is not quite so simple as this.

The viscosity of a solution increases as it is concentrated. Thus a 5 per cent. solution of sucrose has nearly the same viscosity at 0° C. ($\eta = 0.02048$) as a 40 per cent. solution at 50° C. ($\eta = 0.0241$), and has the same viscosity as a 40 per cent. solution at 58° C.[1] It is, however, always possible that the constitution of the protoplasm and its percentage of water may alter as the temperature rises or falls, but within a certain range (0° C. to 40° C.) we are probably justified in assuming that it retains the same average composition during short exposures.

In a rotating cell the question of friction between the surfaces in contact need not be considered, for the friction of a fluid against a smooth surface is independent of the material of the latter if it is wetted by the fluid. The fact that water and solutions of glycerine can pass through the vacuolar membrane to the cell-sap and also outwardly, proves that the cell-sap wets the vacuolar membrane. A liquid flows through a uniform capillary tube in the form of parallel concentric sliding lamellae. Hence when rotation occurs in a plant-cell the vacuolar membrane carries with it the layer of cell-sap immediately touching it. The next layer, however, slips slightly to an extent determined by the viscosity of the cell-sap, the next still more, until a little distance inwards the motion is practically extinguished. An increase in the viscosity of the cell-sap, or in the velocity of streaming, will bring more of the cell-sap into motion, and hence will increase the retarding effect of the latter upon the streaming endoplasm. A rise of temperature increases the velocity of streaming but decreases the viscosity of the cell-sap, the influence of the former being greater than that of the latter upon the bulk and average velocity of rotating cell-sap. Thus at low temperatures when streaming is slow, it is usually difficult to distinguish any translatory movement in the cell-sap

[1] R. Hosking, Phil. Mag., 1900, pp. 274–86.

at all [1]. As the temperature rises and the velocity increases, the outer layers of cell-sap begin to move with increasing speed, but the movement never extends far inwards in large cells. The mechanical moment exercised by rotating fluids in virtue of their viscosity has been investigated by Mallock [2], but in the case of a rotating cell, to determine the force expended in unit time in moving the cell-sap, it would suffice to know the average velocity of the latter, the mass of it moved, and its viscosity.

An increase in the velocity of the endoplasm will not only increase the bulk of rotating sap but will also tend to bring the outer layers of the protoplast into motion. In *Chara* and *Nitella* the ectoplasm and the bulk of the chloroplastids always remain at rest, but in *Elodea*, *Vallisneria*, &c., the whole of the protoplasm and chloroplastids may appear to rotate. The outermost layer must, however, for both physical and biological reasons, remain at rest, and in fact examination with high powers always reveals the existence of a peripheral non-moving layer 'wetting' and adherent to the cell-wall. Hence as the velocity increases, the most actively moving layer travels outwards, and as it decreases moves inwards. Moreover, the velocity falls very rapidly towards the outer non-moving layers, but much more gradually towards the cell-sap. The latter fact points to a relatively high viscosity of the protoplasm as compared with that of the cell-sap.

It is obviously impossible to measure the viscosity of protoplasm directly, but approximate measurements can be obtained by indirect observations, and by comparison with allied substances. Thorpe and Rodger [3] have obtained some very interesting results bearing upon the influence of chemical constitution upon viscosity. Thus in homologous series the viscosity increases as the molecular weight does, but it is also influenced by constitution and complexity. There is, however, no absolute relation between molecular weight and viscosity, while in the case of many proteid substances, a relatively trifling chemical change (coagulation) may enormously increase the viscosity.

The osmotic concentration of the cell-sap is usually equal to from 1 to 3 per cent. KNO_3, and it usually contains less than 5 per cent., rarely more than 10 per cent. of dissolved matter. The viscosity of a watery solution is usually greater than that of pure water. Thus a 21·5 per cent. solution of cane sugar has twice ($\eta = 0{\cdot}0202$), a 30 per cent. three times ($\eta = 0{\cdot}0304$), and a 40 per cent. six times ($\eta = 0{\cdot}0607$) that of water at 20° C. ($\eta = 0{\cdot}01009$). Taking water as unity, the viscosity of normal

[1] The currents in the cell-sap may be rendered more clearly visible by causing the cells to absorb aniline dyes, or producing granular precipitates in the cell-sap by treatment with dilute solutions of ammonium carbonate, or of caffein.

[2] Phil. Trans., 1896, vol. CLXXXVII, p. 41.

[3] Phil. Trans., 1894, Bakerian Lecture.

solutions (one gram molecule per litre) of inorganic salts varies from 1·1 to 1·3, and of organic salts from 1·3 to 1·8. In the case of normal solutions of NH_4Cl, KCl, and KNO_3, the ratio is 0·97, and in that of KI, 0·91 [1], solutions of these substances having a less viscosity than pure water. The decrease is slight, but it increases with the concentration: thus in the case of a 7 per cent. solution of KNO_3, $\eta = 0{\cdot}0169$, in that of a 14 per cent. solution, $\eta = 0{\cdot}0155$. Hence the viscosity of the cell-sap under ordinary circumstances probably lies between 0·01 and 0·02 at 20° C. In cells loaded with sugar (beet-root, onions, &c.) the viscosity may rise to from 0·03 to 0·06 at 20° C., and the retarding or preventive effect of the cell-sap upon streaming or upon any tendency to streaming would be proportionately increased.

From a purely physical point of view protoplasm is to be regarded as consisting mainly of a colloidal albumin containing large and varying percentages of water, the latter having a very pronounced influence upon its viscosity. Hence it is of importance to know the values for colloidal solutions such as ordinary egg- and serum-albumin.

SECTION 7. **Viscosity of Albuminous Solutions.**

Instead of attempting any absolute measurements, the easier method was adopted of comparing the rates of flow of equal volumes of egg-albumin, and of liquids of known viscosity through a capillary tube under the same pressure and in the same direction. The albumin was obtained from fresh eggs, snipped in all directions with sharp scissors, and then filtered under pressure through linen in order to remove its ropy character. The first samples used contained from 89·4 per cent. to 89·9 per cent. of water, their density being 1·042.

In a particular experiment [2] with 99 per cent. glycerine of density 1·2612 (at 19·3° C.) the time of flow was 43 min. 20 secs. at 18·5° C., and of the same volume of egg-albumin 120 secs. at 18·5° C.

Now $\eta : \eta' :: td : t'd'$, where η and η', are the viscosities of the albumin and glycerine respectively, t and t′ their times of flow, and d and d′ their densities. Substituting these values and the known viscosity of glycerine at this temperature, $\eta = 0{\cdot}381$.

When, as in this case, the difference of velocity is very great, various errors are introduced. Thus the resistance instead of increasing in direct proportion to the velocity, may increase as a power of the speed rising to as much as 1·8, so that in comparison with the more viscous glycerine, the albumin appears to have a higher viscosity than is really the case. Thus

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[1] Landolt and Bornstein, Phys. Chem., Tabellen, p. 293.

[2] In all cases the time of out-flow was taken, and the lower end of the capillary kept immersed beneath the liquid, so as to avoid the formation of drops and consequent errors due to their surface-tension retarding the out-flow. (See Fig. 4, p. 21.)

deducing the viscosity of water from the relative rates of flow of it and of glycerine gave a value for water at 18° C. of 0·0025, which is the viscosity of a 7·2 per cent. solution of Na_2SO_4 at 0° C., whereas the real value for water is 0·010672, or less than half that found by comparison with glycerine.

In an experiment with water and egg-albumin the relative times of flow were 118 secs. and 648 secs. at 18·5° C., which gave a value for egg-albumin of $\eta = 0{\cdot}057$. Owing to the slower flow of the albumin its viscosity will, however, appear to be less in comparison with water than it really is.

The viscosity of aniline at 20° C. is 0·04467 and hence its rate of flow should not differ very much from that of the egg-albumin. The average time of flow of aniline was 232 secs. at 18° C. and of albumin 377 secs. Their densities being 1·039 and 1·042 respectively a value for η of 0·073 is obtained. Another set of experiments at 18·5 gave a value of $\eta = 0{\cdot}0701$.

The times of flow of various samples of egg-albumin containing 89 to 91 per cent. of water lay between those of solutions of sugar of 38 to 41 per cent. strength at 18° C. Allowing for the respective densities, this gave values for η lying between 0·06 and 0·07. It follows, therefore, that the viscosity of an albuminous solution is much higher than that of saline or sugar solutions of the same concentration.

The addition of sufficient dilute saline solution to reduce the quantity of albumin to 5 per cent. lowered the viscosity to 0·042, while the viscosity of a solution containing 72 per cent. of water rose to 0·292 [1]. Similar experiments with defibrinated blood-plasma (serum-albumin and salts) of the rabbit and sheep gave viscosities lying between $\frac{1}{2}$ to $\frac{2}{3}$ of those of egg-albumin containing corresponding percentages of water. In solutions containing 5 per cent. of serum-albumin $\eta = 0{\cdot}022$; with 18 per cent. of serum-albumin $\eta = 0{\cdot}19$ [2].

Living protoplasm may contain from 10–30 per cent. of solids, the percentage probably lying near the lower limit in the endoplasm of rotating cells. In all cases, however, solid floating particles are present, and the influence of these upon the viscosity cannot be directly determined. We have, however, weighty reasons for considering the viscosity of the main bulk of the streaming protoplasm to lie within the limits $\eta = 0{\cdot}04$, and $\eta = 0{\cdot}2$ at 18° C.

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[1] Perfect accuracy and constancy is not claimed for these numbers, but it is useless to introduce small corrections when dealing with a material whose viscosity varies according to its origin and previous treatment.

[2] Few or no data on the viscosity of solutions of serum-albumin or of blood-plasma are given in textbooks of animal physiology, although this is a factor of the utmost importance in determining the resistance offered to the circulation of the blood, and hence the work done by the heart. In the case of poikilothermic animals the viscosity of the blood-plasma will be largely influenced by the temperature of the surrounding medium, whereas in mammals and birds the temperature effect will be constant except in cases of heat-pyrexia. The nature of the containing walls does not affect the resistance to flow, so long as the lining epithelium is relatively smooth.

SECTION 8. Influence of Temperature on Viscosity.

With very few exceptions the viscosity of a solution decreases as the temperature rises, and each substance has its own specific rate of decrease. The influence of temperature on the viscosity of albumin was investigated by means of the apparatus shown in Fig. 3. The flask A contains either brine cooled by a freezing-mixture, or water heated to any required temperature. This can be siphoned to and fro through the water-jacket B by means of an adjustable reservoir (as at F) attached to D. By lowering the mercury reservoir F, albumin from K is drawn up to the mark C, and the clip N closed. The mercury in F is then raised, and when it has ceased to flow into E, and the temperature in B is constant, the clip N is opened, and the time the albumin takes to fall to the mark H is noted. The volume CH is very much less than that of E or F, and hence the pressure is practically uniform throughout, while since the velocity is low and the differences of velocity small, the viscosities are directly proportional to the times of flow.

The apparatus was first tested by calculating the viscosities of sugar solutions and of dilute glycerine of known strength at different temperatures from their relative times of flow and the values for one of them given in Landolt and Bornstein's 'Tabellen.' A series of experiments were then made with egg-albumin, prepared as previously described, each of the figures given being the average of three experiments.

Temperature.	Time of flow[1].	Difference of temperature.	Difference per 1° C. in time of flow.	Viscosity.	
				Albumin.	Water.
3° C.	212 secs.			0.107	0.016214
10°	168 ,,	7° C.	−6.28	0.085	0.013257
18°	144 ,,	8°	−3.0	0.073	0.010672
27°	122 ,,	9°	−2.4	0.062	0.008625
45°	96 ,,	18°	−1.4	0.049	0.006131
60°	80 ,,	16°	−1.0	0.040	0.004865
63°	104 ,,	3°	+8.0	0.053	0.004653
65°	216–228 ,,	2°	+56 to 62	0.109–0.115	0.004521
70°	...	5°	...	...	0.004239

The viscosity of egg-albumin containing 10·8 per cent. of solids steadily decreases up to 60° C., although the decrease becomes less and less per degree as the temperature rises. Above 60° C. the viscosity increases, and at 65° C. it is greater than at 3° C., while at 70° C. the coagulation stops all flow. Hence a rise of temperature within certain limits will directly accelerate streaming independently of any increased energy of respiration, and that to no small extent since a rise of temperature from 0° C.

[1] The rapid rate of flow is necessary owing to the difficulty of maintaining the temperature absolutely constant for any length of time.

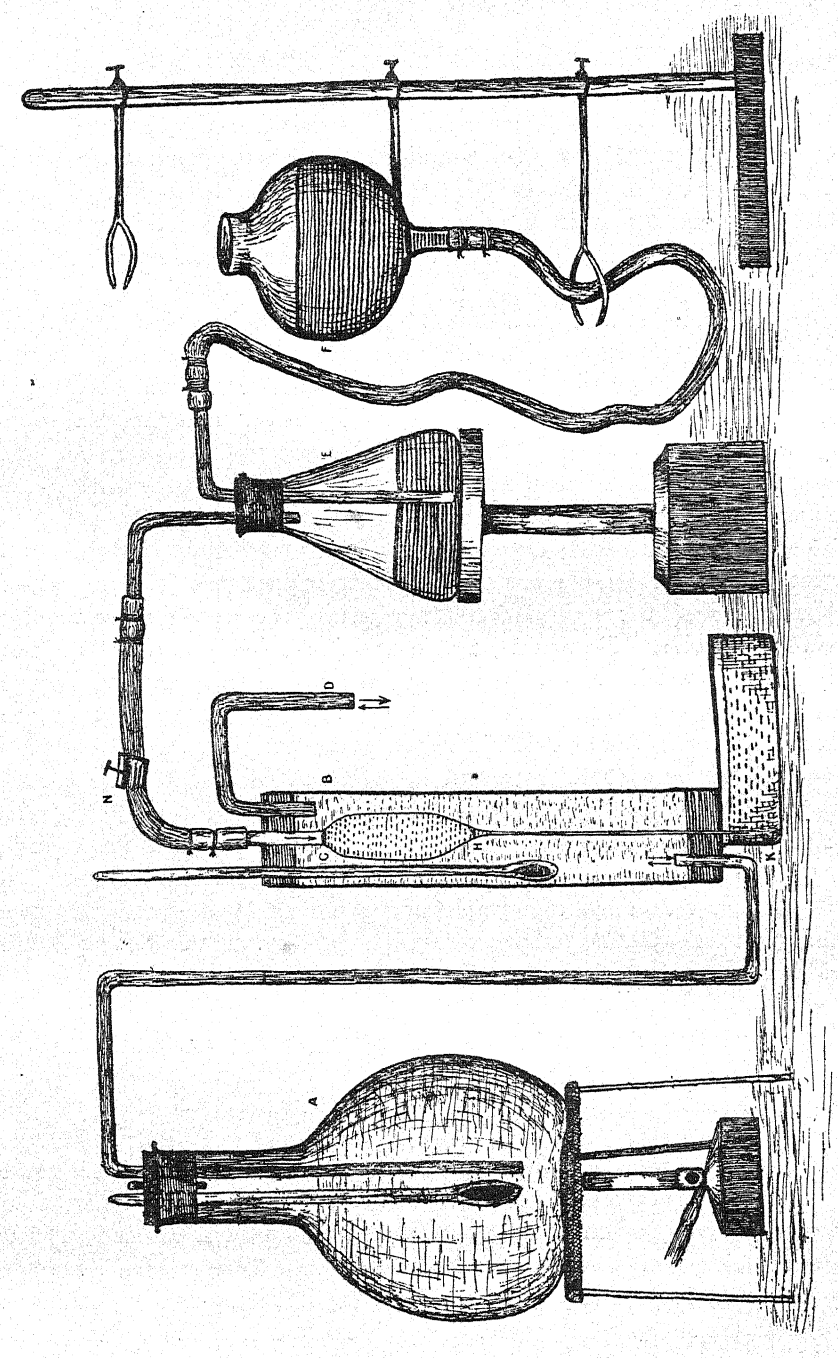

FIG. 4. Apparatus for determining the influence of temperature on viscosity.

to 45° C. may cause the viscosity to decrease to one-third its previous value.

In a cell of *Nitella* the times taken to cover a space of 1 mm. at 18° C., 27° C., and 45° C. were 54 secs., 38 secs., and 25 secs. respectively. These velocities bear ratios of 1·3, 1·6, and 1·9, to the velocities deduced from the velocity at 10° C., by allowing for the viscosities of egg-albumin at 10° C., 18° C., 27° C., and 45° C. Apparently, therefore, the velocity of streaming increases in a greater ratio than the viscosity of egg-albumin or water decreases. This is probably due to the increased respiratory activity at the higher temperatures rendering more energy available, and hence increasing the propulsive force, although only a small fraction of the total energy of respiration is ever utilized in producing streaming movements.

Similar ratios were given by *Chara*, *Elodea*, and *Vallisneria*, and they suffice to show that the influence of temperature on viscosity is always a very important factor in the kinetics of the cell, while the decrease in viscosity due to a rise of temperature is probably mainly responsible for the increase of velocity between 0° C. and 30° C.

The fact that the plasma probably contains a variety of proteids does not affect the general issue, since the temperatures selected for comparison are all well beneath the coagulation temperature of even the most readily coagulable proteids. Except in the case of solutions of KNO_3, dilute watery solutions all decrease in viscosity when heated, and the amounts of decrease bear approximately corresponding ratios to those in the case of water, so long as the solution is not over 10 per cent. strength. This also applies to egg-albumin, as can be seen by reference to the preceding table.

The increase in viscosity of egg-albumin occurs at too high a point (63°–65° C.) to explain the retardation and ultimate cessation of streaming at 50°–55° C., and its almost immediate stoppage at 55° C.–60° C. In this connexion the coagulation temperatures of the chief varieties of coagulable proteids are of interest, thus:—

Serum-albumin	coagulates at from 70° C.–80° C.
Paraglobulin	,, ,, ,, 70° –75°
Plant-albumin and egg-albumin	,, ,, ,, 65° –70°
Myosinogen and fibrinogen	,, ,, ,, 55° –60°

Myosinogen, and probably fibrinogen also, do actually occur in plant protoplasts, and hence there is every reason to suppose that the retardation of streaming at high temperatures is due to slight partial coagulation of these proteids, and possibly of allied ones also. The sudden stoppage at 55° C.–60° C. is probably due to their complete coagulation. Various signs of this are shown when the stoppage is not too rapid, as for example, the jerkiness and irregular character of the movement before it ceases, the

frequent temporary formation of subsidiary obliquely directed 'currents,' and occasionally a change in the plane of movement. The presence of only a small amount of readily coagulable proteid will suffice to cause a stoppage of streaming at its coagulation point, just as a small amount (0·2 per cent.) of fibrinogen causes the clotting of blood when it turns into solid fibrin.

Cells which have been exposed to 50° C.–55° C. for a short time may recover, and show fairly active rotation at normal temperatures. Frequently, however, the original rapidity is not regained for some time, and the activity of streaming is in some cases permanently depressed. The plasma of such cells may show a distinct tendency to ball together, and the streaming layers may contain irregular transparent masses often with imbedded chloroplastids. These masses are probably formed by partially coagulated proteids and may subsequently disappear, apparently being broken up and reabsorbed.

SECTION 9. **Influence of Gravity on Rotation.**

To drive the same bulk of liquid upwards through a capillary in the same time as when it is driven downwards requires a greater pressure, or takes a longer time if the pressure is constant. The difference of pressure is proportional to the density of the liquid, the relative velocities of flow, and the force of gravity. It does not follow that a corresponding difference will be observed between the ascending and descending streams in a cell placed with its long axis vertical, even in the absence of any physiological response to gravity. For in a closed system of this kind, the action of gravity counterbalances on the two sides. Thus in a series of observations made upon small more or less cubical cells of *Elodea* and *Vallisneria* no constant difference of velocity could be observed between the ascending and descending streams. Frequently the endoplasm became thicker at certain points, and these thickenings circulate several times around the cell before thinning out again. If they are very marked, irregular variations of velocity ensue. In the case of large elongated cells, gravity seemed apparently to exercise a distinct influence upon the velocity of streaming. The action was immediate and was not preceded by any perceptible latent period, or by any after effect. Any stimulating action, it should be noticed, would necessarily be slightly greater upon the ascending than upon the descending stream. The observations were made upon large elongated leaf-cells of *Elodea* and *Vallisneria*, upon end cells of *Chara*, and upon internodal cells of *Nitella*, in which the direction of streaming was more or less closely parallel to the long axis of the cell.

The velocity of streaming can only be told by observing the time taken by a floating particle to cross a measured space on a micrometer

scale projected on to the field. The time was estimated by the aid of a metronome, thus leaving the eye free to follow the particle. Only particles of a certain size and character were observed at a given time, and only the times of those which kept to the marked track were taken. The velocity of the stream varies at different depths, and hence the observations were made under the high power, which was kept focussed as closely as possible to a measured constant depth beneath the non-rotating ectoplasm. A large number of observations (10–20) were taken first on one side of the indifferent line or of the cell, and then on the other, and the mean of these found.

These results are, however, liable to vary, since the general velocity may alter during the time of observation, and since the velocity is not always uniform throughout.

The following data were obtained from a cell of *Nitella*:—

Temperature, 17·5° C.; beats of metronome, 175 in 60 secs.; distance traversed, 0·275 mm.

	I. Mean of Metronome beats.	Mean Velocity.	II. Mean of Metronome beats.	Mean Velocity.
Upward side[1] .	24·3	1·99 mm. per min.	24·6	1·96 mm. per min.
Downward .	22·875	2·13 ,,	22·4	2·15 ,,
Before	23·1	2·08 ,,	23·3	2·06 ,,
When horizontal				
After	23·2	2·07 ,,	23·2	2·07 ,,

The same relative rates were shown after the lapse of half an hour, and no measurable thickening of the apparently more slowly rotating portion could be noticed, as must have occurred if the velocity of the particles accurately represented that of the fluid plasma. Two conditions for accurate observations are (1) that a constant source of illumination should be used, and the percentage of radiant heat reduced as far as possible; (2) that an optimal supply of oxygen should be assured.

The observations are less open to error if the same region is observed, and its position in space altered by tilting the stand until the stage is vertical and rotating the latter until the object is reversed. Successive series of readings may be taken, or the object may be reversed after each observation.

Nitella (17·5° C.).

	Successive observations.	Alternating.	End cells of *Chara*.
Up	1·958 mm. per min.	1·95 mm. per min.	2·02 mm. per min.
Down . . .	2·2 ,,	2·17 ,,	1·84 ,,
Horizontal .	2·16 ,,	2·09 ,,	1·98 ,,

By taking alternating sets of successive observations fairly constant results are obtained for each particular cell by observing similar particles.

[1] Under the microscope the directions are of course reversed.

Nitella (18·5° C.).

	I.	II.	III.
Up	2·83 mm. per min.	2·92 mm. per min.	2·78 mm. per min.
Down . . .	3·14 ,,	3·15 ,,	3·1 ,,
Horizontal .	3·06 ,,	3·08 ,,	3·02 ,,

Similar results were obtained with elongated cells of *Vallisneria* and *Elodea* at 17° C., the figures given representing the velocities in mm. per min.

Vallisneria.

	I.	II.
Down . . .	0·752 } Mean velocity, 0·712	0·736 } Mean velocity, 0·702
Up	0·672 }	0·668 }
Horizontal .	0·721	0·716

Elodea.

	I.	II.
Down . . .	0·972 } Mean velocity, 0·962	0·954 } Mean velocity, 0·924
Up	0·952 }	0·895 }
Horizontal .	0·965	0·928

In both the latter plants a curious anomaly may often be observed if floating chloroplastids or oil globules are used to indicate the velocity of the streaming plasma, for they sometimes appear to indicate more rapid streaming upwards than downwards. Thus: down, 0·954 mm. per min.; up, 0·989 mm. per min.

In nearly all cases it will be noticed that the difference between the horizontal velocity and the upward velocity is greater than the difference between it and the downward velocity, the mean velocity in a cell placed with its long axis vertical being slightly less than when it is horizontal.

	Mean velocity in vertical position in mm. per min.		In horizontal position.	
	I.	II.	I.	II.
Vallisneria .	0·712	0·702	0·721	0·716
Elodea . . .	0·962	0·924	0·965	0·928
Nitella . . .	2·98	2·94	3·06	3·02

A difference of velocity is no longer perceptible in cells of *Chara* and *Nitella*, in which the direction of rotation is in a plane cutting the long axis of the cell at an angle greater than 15 to 20 degrees.

It is possible that gravity exercises a very slight and barely perceptible physiological retarding action in streaming when elongated cells are placed vertically, and that by very powerful centrifugal forces a marked retardation, or even a cessation of streaming, might be induced. The apparent differences of velocity observed in the ascending and descending streams have, however, mainly a purely physical origin. They are due to the particles observed being different in density to the liquid in which they

float, heavy particles ascending slightly less rapidly than the upward stream, but descending more rapidly in the downward stream. With particles of lesser density (oil globules, &c.) the reverse is the case. Suppose that the true velocity of the stream is V mm. per min., and the velocity of slip of a denser particle U mm. per min. Then, if the particle has an apparent velocity of 2·83 mm. per min. in the ascending, and 3·14 in the descending stream :—

$$V + U = 3{\cdot}14\,;\quad V - U = 2{\cdot}83$$
$$\therefore\ V = 2{\cdot}98 \text{ and } U = 0{\cdot}15 \text{ mm. per min.}$$

Neither the density of the plasma, nor that of the floating particles, can be calculated with sufficient accuracy to enable the viscosity of the protoplasm to be deduced from the velocity of slip of denser or lighter particles. The differences of velocity are by no means always as pronounced as the above, but they suffice to indicate that the viscosity of the streaming endoplasm cannot be very great since its density and that of the denser floating particles only differ to a slight extent. Moreover the above facts point strongly to the conclusion that the visible floating particles are passively carried by the streaming plasma, and neither propel themselves nor it.

SECTION 10. **The Energy expended in a Streaming Cell.**

The problem in the case of a large cell of *Nitella* may be stated in the following simplified form. A cylinder AB with rounded ends is bounded externally by a thin homogeneous membrane 0·05 mm. thick (Fig. 5, p. 28). Within this is a very viscous non-moving layer EF, and internally to the latter is a less viscous layer FG streaming steadily round the cell parallel to its long axis, the motion being reversed in the opposite halves of the cell. Centrally is water containing inorganic salts, and frequently sugar, &c., in solution. The outer layers of water also move in the same direction as the living layers they touch, but more slowly, and with a velocity which rapidly decreases to *nil* towards the centre of the cell. The following are the dimensions : AB = 20 mm. ; CD = 1 mm. ; EF = 0·05 mm. ; FG = 0·1 mm. ; GH = 0·6 mm. The motion is most rapid (3 mm. per minute) just to the outside of the median point of FG, thence decreasing rapidly externally and less rapidly internally.

The volume of the streaming plasma is 6 cubic mm. approximately, and its average velocity is slightly over 2 mm. per minute. The volume of the cell-sap is 5 cubic mm., and its average velocity 1 mm. per minute.

The endoplasm takes eight minutes to complete a rotation.

Hence in one minute $\frac{6}{8}$ cubic mm. of the plasma and $\frac{5}{16}$ cubic mm. of the cell-sap pass a section across the cell.

If we suppose the streaming endoplasm to correspond to egg-albumin containing 90 per cent. of water, its viscosity will be approximately 0·075

at 18° C. That of the cell-sap will not be higher in the case of *Nitella* than 0·025.

Hence we may suppose that in each minute $\frac{3}{4} + (\frac{5}{16} \times \frac{1}{3}) = 0{\cdot}85$ cubic mm. of liquid of viscosity 0·075 pass a given section. This equals 0·000,014 cubic cm. per 1 second.

Now in the case of a liquid driven by pressure through a capillary tube, if η = the viscosity in dynes per sq. cm. (0·075);

r = radius of capillary in cms. (0·04), and l = its length (2 cm.);

v = volume passed per second in c.c. (0·000,014);

p = pressure in dynes per sq. cm.

Then $p = \frac{8\,\eta\,v\,l}{\pi r^4} = \frac{8 \times 0{\cdot}075 \times 0{\cdot}000{,}014 \times 2}{3{\cdot}141{,}6 \times 0{\cdot}000{,}002{,}56} = 2{\cdot}1$ dynes per sq. cm.

Taking the density of the plasma as 1·2, 2 cubic centimetres would weigh 2·4 grams.

Hence per gram of plasma a force of $\frac{2\,1}{2{\cdot}4} = 0{\cdot}875$ dyne is required to impart a velocity of 2 mm. per minute.

At this velocity a centimetre is covered in 5 minutes. Hence in 1 day $\cdot 875 \times 12 \times 24 = 252$ ergs of work are done.

Taking the mechanical equivalent of heat as $4{\cdot}18 \times 10^7$ ergs.

252 ergs correspond to $\frac{252}{4{\cdot}18 \times 10^7} = 0{\cdot}000{,}006{,}05$ gram-calorie.

But one gram of plant-fibrin yields 5,900 calories when burnt.

Hence a minimum consumption of $\frac{0{\cdot}605}{59 \times 10^7} = \frac{0{\cdot}102}{10^8}$ gram of plant-fibrin or $\frac{0{\cdot}105}{10^8}$ gram of albumin (heat eq. = 5,700) would be required per day, if the protoplast were a perfect machine. If glycerine, starch, cane sugar, lactose, or dextrose [1] were consumed, about $1\frac{1}{2}$ times as much would be required. Hence to keep a gram of endoplasm of viscosity 0·075 moving with a velocity of 2 mm. per min. in a cell of the dimensions given requires only a theoretical consumption of $\frac{55{\cdot}8}{10^8}$ or $\frac{1}{200{,}000}$ of a gram of cane sugar *per annum*, an amount so small as to be negligible.

That the plasma has not a high viscosity is shown by the pronounced action of gravity upon floating particles whose density differs but little from that of the plasma. But even if the viscosity were as high as that of a solution of egg-albumin containing 72 per cent. of water (0·29) the theoretical consumption of energy would only be increased fourfold, and would represent 0·00002 gram of sugar per gram of plasma per year. An

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[1] One gram of glycerine produces 4,200 calories; starch and cellulose, 4,100; cane sugar, 4,000; lactose, 3,900; dextrose, 3,700, when burnt into carbon dioxide and water.

actively respiring protoplast may, however, produce carbon dioxide at the rate of over 10 grams per gram per year, which represents a consumption of 22 grams of sugar per annum. Hence the amount of energy consumed in the streaming movements within large cells such as those of *Chara*, *Nitella*, &c., forms an inappreciable fraction of that produced by respiration, even if the motor-mechanism is so imperfect as to waste 99 per cent. of the energy supplied.

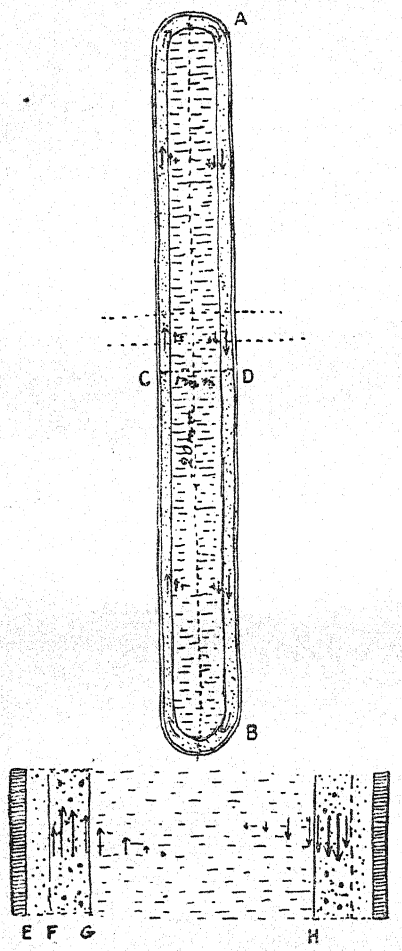

FIG. 5. A. Diagram of streaming cell of *Nitella*, major axis five, and minor axis ten times enlarged. B. Section across the same magnified 50 diameters.

In cells with smaller radii, however, the resistance to flow increases disproportionately. The force in dynes per sq. cm. required to drive the same volume of liquid through capillaries of the same length but with dissimilar radii is inversely proportional to the 4th power of the radius (πr^4). But if the velocity of flow is constant, the volume passing is directly proportional to the sectional area (πr^2). Hence the force required varies inversely as r^2.

Therefore if a force of ·875 dyne is necessary to move a gram of liquid through a tube of 0·1 cm. diameter at a velocity of 2 mm. per minute, a force of 21·9 dynes will be necessary to drive a gram of fluid through a tube 0·01 cm. diameter at a velocity of 0·4 mm. per minute. In cells whose internal diameter approaches 0·01 cm. the average velocity of the cell-sap and plasma is rarely more than 0·4 mm. per minute.

At this velocity a centimetre is covered in 25 minutes.

Hence per day $\frac{21{\cdot}9 \times 12 \times 24}{5} = 1{,}251{\cdot}8$ ergs of work are done per gram of moving liquid.

This represents $\frac{1{,}251{\cdot}8}{4{\cdot}18 \times 10^7} = \frac{3}{10^5}$ gram-calorie, or a consumption of $\frac{3}{4 \times 10^8} = {\cdot}000{,}000{,}007{,}5$ gram of cane sugar per gram of moving liquid per day.

But an actively respiring seedling may produce from 1 to 2 per cent. of its weight of CO_2 per day, which corresponds roughly to a consumption of 0·017 to 0·034 gram of cane sugar per day per gram of protoplasm. Hence in cells approaching 0·01 cm. diameter, even if only 1 per cent. of the energy directed towards streaming is actually utilized, the whole amount expended does not form more than $\frac{1}{10000}$ of the energy represented by moderately active respiration. In ordinary plant-cells, therefore, it seems certain that much less than a tenth of a per cent. of the energy of respiration is consumed in producing streaming movements.

In the case of a tube of 0·001 cm. internal diameter, a consumption of 100 times as much energy would be required as in one of 0·01 cm. diam. to produce the same velocity of flow. This might represent as much as from $\frac{1}{10}$ to 1 per cent. of the energy of respiration, and herein probably lies the reason for the absence of streaming movements in small young cells, and their gradual commencement and increase in velocity as the cell grows larger and older. In any case it is of importance to remember that the influence of the diameter of the cell upon the resistance to streaming is much greater than that of any possible changes of viscosity, the ratio between the two factors being as $\frac{1}{r^2} : \eta$.

Resistance to Flow in Protoplasmic Threads.

In the case of the interprotoplasmic connexions passing through minute channels in the cell-wall, the diameter is excessively small, and hence the resistance to flow very great. Suppose a thread to be $\frac{1}{20}$ μ diameter and 5 μ length, then a pressure of 6 atmospheres would be required to move a liquid of viscosity 0·075 through it with a velocity of 1 mm. per second, taking one atmosphere as equal to 1,000 grams per sq. cm. The viscosity of the ectoplasm is certainly very much higher than the values given, and the minutest solid particle would suffice to block the thread. The smallest difference of surface tension at the ends or middle of the thread would interpose a very great resistance to flow. Thus if a tissue-cell were isolated in air it would need a pressure of 34 atmospheres to overcome the resistance due to the surface tension of a drop of water escaping from a thread of $\frac{1}{10}$ μ diameter. Even in water or in the intact tissue the total energy of respiration in the plasma of the thread would hardly suffice to overcome the resistance due to these various sources, although differences in the osmotic pressure of neighbouring cells might be more efficient in this respect. But usually the osmotic pressure in neighbouring cells differs only by a fraction of atmosphere, and hence by this means it would hardly be possible to induce movements in mass at a greater rate than 1 mm. per day. At this speed it would

take 100 years for the escape of 1 cubic mm. of the cell-contents through 3,000 threads of $\frac{1}{10}$ μ diameter. Hence it is safe to conclude that no streaming movements in mass take place through the interprotoplasmic connexions of neighbouring cells, these structures serving for the conveyance of physical and chemical impulses (stimuli), and the transference of solid materials taking place almost entirely by the diffusion of liquids through the cell-wall. In the case of the short broad pores of sieve-plates, however, comparatively small differences of pressure would suffice to induce slow movements in mass through the pores. Thus in the series of 2,000 sieve-plates, each with sieve-pores of 2 μ diameter and 10 μ length, included in 50 cms. of the cribral system of *Cucurbita*, a pressure of about half an atmosphere would be needed to produce a movement in mass of the more watery contents through the tubes at an average rate of 5 mm. per minute, so long as the pores remained unblocked. This corresponds with the slow exudation which takes place when the tubes are first opened.

For the above reasons it is hardly probable that any perceptible streaming movements occur in Bacteria, in spite of the remarkably active transformations of energy of which these organisms are capable.

In the case of protoplasmic threads crossing the vacuole within a cell, the conditions are very different, for the flow does not take place in rigid tubes with fixed walls. The plasmatic membrane moves with the stream, and hence only the friction against the cell-sap, which is of low viscosity, need be considered. In a cell exhibiting circulation, the total resistance to flow will be somewhat greater than in one in which the protoplasm rotates around a single central vacuole. Hence arises in part at least the increase in the average velocity when circulation changes into rotation.

Calculation of work done from coefficient of friction.

The coefficient of friction between a smooth metal plate and water is at room-temperature 0·23 lb. per sq. foot at a velocity of ten feet per second. If the cell-wall (or ectoplasm) is considered as a flat smooth plate moving through a liquid having ten times the viscosity of water, it is possible to calculate the drag upon it, and hence the relative magnitude of the force inducing movement.

A cell 2 cm. long and of 0·1 cm. internal diameter has an external surface of 0·659 sq. cm. ($2\pi r l + 2\pi r^2$). But the friction between the liquid in question and a smooth plate would be equal to $\frac{1}{80}$ of a dyne per sq. cm. at a velocity of 2 mm. per minute, that is, ·08 dyne per 0·659 sq. cm.

But the volume of the moving plasma is 6 cubic mm., and the mass of it moving is 0·072 gram approximately. Hence per gram of plasma a force of 1·1 dynes is required.

At a velocity of 2 mm. per minute, 0·22 erg of work would be done per minute per gram of moving plasma, instead of the 0·18 erg per gram per minute as calculated in the case of the same liquid flowing through a capillary tube of 0·1 cm. diameter. This slight discrepancy is not surprising considering the dissimilar modes of calculation.

On a somewhat similar basis O. Müller[1] has calculated that the work done by the protoplasmic band of a diatom against the friction of the surrounding water varies from 56,285 to 830,413 $\delta\,\mu$ units of work per second ($\delta = \frac{1}{1{,}000{,}000{,}000}$ milligram). This equals from 0·000,000,005,6 to 0·000,000,008 erg. But it would take about 400,000 of the diatom *Nitzschia sigmoidea* to make one cubic centimetre.

Hence if we take the density of the diatom as being 2 (Müller, l. c.), and if the streaming plasma forms $\frac{1}{3}$ of the bulk, then the work done per gram of moving plasma would be 0·564 to 0·864 erg per minute, values higher than those given above. The diatom in question moves with an average rapidity of 1 mm. per minute (cf. *Vallisneria*), and Müller has calculated that the velocity of streaming in the external bands must be about 3 mm. per min. (cf. *Nitella*).

SECTION 11. The relation between the work done in streaming and the consumption of energy.

The amount of energy that can be expended upon a partial function such as streaming must always be strictly limited, and the ratio between the total energy of respiration and the amount expended in streaming varies in different plants, and in the same plant at different temperatures and under different conditions. Nevertheless, the minimal amount of oxygen-respiration at which streaming can remain active in an aerobic plant will afford some indication as to the maximal amount of energy that could possibly be expended in this way. Stich found that oxygen-respiration continues, though weaker than usual, at a partial pressure of oxygen corresponding to 20–30 mm. of mercury (3–4 per cent. oxygen), while Clarke has shown that streaming commences at a partial pressure of from 1 to 4 mm. of mercury, and becomes fairly active before the pressure reaches 10 to 15 mm.[2]

A few determinations of the respiratory activity of *Chara* were made in the following manner. Plants were placed in a darkened vessel con-

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[1] Ber. d. D. Bot. Ges., 1896, Bd. XIV, p. 117.

[2] Stich, Flora, 1891, p. 13; Clarke, Ber. d. D. Bot. Ges., 1888, p. 273.

taining well-aerated water, which was then covered by a layer of oil. By means of a syphon-tube measured volumes of the water were drawn off at stated intervals and run into a titrated solution of barium hydrate. The clear liquid from the latter was then titrated with oxalic acid, using phenolphthalein as an indicator. By means of a side tube connected with the long arm of the syphon, reduced indigo solution could be added to the issuing water, and the presence or absence of free oxygen in it detected. The experiments were continued until no free oxygen was present.

On reducing the results to terms of a single cell it was found that 0·754 cubic mm. of protoplasm, of which 0·471 were actively streaming, produced a maximal amount of 0·000336 to 0·000472 mgr. of CO_2 at 18° C. In another case 0·14 to 0·08 mgr. of CO_2 were produced at 17·5° C. per gramme of plasma per hour, whereas actively respiring tissues of Phanerogams may evolve per gramme of plasma from 0·2 to 2·0 mgr. of CO_2 per hour. Rotation continues in *Chara* even when the surrounding water contains no free oxygen, i. e. when the production of carbon dioxide sinks to from $\frac{1}{8}$ to $\frac{1}{15}$ of the above values. The theoretical consumption of energy in producing streaming in a cell of *Chara* or *Nitella* (p. 27) represents less than 0·0001 per cent. of the total energy of active respiration, and hence only a fractional amount is utilized for streaming, even when respiration is at its lowest ebb. Further, the production of carbon dioxide is not a perfectly safe guide as to the amount of energy liberated by katabolism, since this must largely depend upon whether proteids, carbohydrates, or fats are consumed in respiration, as well as upon the amount and character of the by-products. Moreover, katabolism need not always lead to a production of carbon dioxide, and the latter may even involve an absorption instead of a liberation of energy, viz. decomposition of oxalic, citric, and malic acids. In all cases the values obtained for the consumption of energy in streaming are the minimum possible for this particular function on the assumption that the motor-mechanism is a perfect one. Since, however, certain other functions must always coexist, the net consumption of respiratory material must always be very much greater than this. Moreover, the protoplast appears to be a very imperfect machine, for Rodewald[1] has shown that, as far as calculations based upon the production of carbon dioxide can be relied on, by far the greater part of the energy of respiration appears in the form of heat by conduction, radiation, and evaporation. We may regard the protoplast as a machine capable of performing several different kinds of work simultaneously, but never exercising its full potential capabilities in all of them at the same time, and usually all being carried out below their

[1] Jahrb. f. wiss. Bot., 1889, XX, p. 275. In one case 220 grams of Kohl-rabi evolved at 20° C. 0·6070 gram of CO_2 in 59 hours, and lost 70 calories per hour.

optimums. It is to this peculiarity that the remarkable accommodatory powers of the protoplast are due, and they form one of the essential fundamental bases of life in general. Similarly, we may safely assume that the energy actually used in streaming represents a much greater consumption of respiratory material than would theoretically be necessary. A great part of this energy may never find expression in the form of rotation but directly appear as heat, while the major part of the energy inducing streaming, since it is employed in overcoming friction, is ultimately also converted into heat and radiated in this form.

If we consider a rotating cell as a machine for converting potential into kinetic energy, then in comparison with a steam-engine it is an extremely inefficient one, for in a good marine engine from 10–12 per cent. of the energy of the coal consumed may be converted into mechanical work. It is still less efficient in comparison with striated muscle, for in the latter one-fourth (25 per cent.) of the energy may appear as mechanical work and three-fourths as heat when maximal work is being done. At low temperatures the vital mechanism is much more efficient than at high ones, for above a certain optimum, growth and movement are retarded and ultimately cease, whereas respiration continues to rise up to, or almost up to, the lethal temperature, when it either falls abruptly to *nil*, or suddenly ceases. The retardation and ultimate sudden stoppage of streaming at high temperatures, though partly a shock-effect under certain conditions, is undoubtedly mainly due to the commencing coagulation of the more coagulable forms of proteid present in the cell. The consequence is that the friction between the particles of plasma rapidly increases, and streaming ceases before it is completely coagulated. In the same way, when an entire steam engine is heated, the decomposition of the lubricating oil, the irregular expansion of tightly-fitting parts, and the change in character of the polished friction surfaces, all interpose an increasing frictional resistance to motion, which slows and ultimately ceases, although the engine may be consuming more fuel than when it is in active motion. There are, however, two essential differences between the mechanisms in the two cases, for the protoplasm may, on occasion, derive energy from the consumption of portions of the motor mechanism, and it is certainly not a thermo-dynamic machine.

SECTION 12. **Direction of Streaming and Path of Least Resistance.**

In protoplasmic threads the direction is rarely constant for any length of time, but changes as the configuration alters. When the entire endoplasm rotates around a central vacuole, however, the same direction of rotation is usually maintained under normal conditions during the entire

life of the cell. According to Berthold[1], the plane of rotation is always constant, being parallel to the surface of the leaf in *Vallisneria*, and at right angles to the surface in the cortical cells of *Chara*. The plane of rotation can, however, be artificially altered by the death of neighbouring cells, by localized injuries (heat, intense illumination) to particular cells, and by exposing cells which have been kept in darkness for some time to strong light (*Elodea*). Similarly, a change in the direction of streaming can sometimes be observed in cells of *Vallisneria* and *Elodea* after the application of stimuli sufficiently powerful to cause a permanent stoppage and death in some cells, and a temporary stoppage in the rest. No such reversal ever seems to occur in *Chara* or *Nitella*, although it is possible, by producing localized light or heat rigor at the middle of a cell, to break the stream into two halves circulating in the unaffected ends.

According to Berthold (l. c., p. 122) there is no constant relation between the direction of streaming in contiguous cells of *Vallisneria* and *Elodea*. This is an error, for almost without exception, the direction of streaming is opposed on the two sides of each dividing wall, i.e. is either with or against the hands of a watch in all the cells of a leaf.

A curious type of streaming sometimes occurs. The plasma streams along a single large strand crossing the vacuole, and, spreading out like a fountain jet, returns along the opposite side walls of the cell. It occurs in hairs of *Cucurbita*, young endosperm cells of *Ceratophyllum* (Velten), and in the young segments of the wood vessels of *Ricinus* (de Vries)[2].

The central strand may be connected to the peripheral layers by thin lateral strands, and this type may pass into ordinary circulation.

Alex Braun[3] showed that the order of development of lateral leaves and roots in *Chara* bore a definite relation to the direction of streaming in the parts from which they rise, those to which the stream is directed developing first. This is probably largely a question of nutrition, for there can be no doubt that streaming in the large cells of *Chara* and *Nitella* is of the utmost importance for rapid translocation. Indeed, Hörmann[4] concludes that the spiral streaming in the larger cells of *Chara* and *Nitella* is an adaptation to favour translocation. That lateral diffusion to and from the medullary cells of *Chara* may be accelerated by the spiral direction of the streaming layers in the cortical cells is obvious, but it is not easy to see how longitudinal transference can be accelerated by the adoption of a longer path. It is impossible, moreover, to follow Hörmann in his attempts to deduce physiological conclusions, unsupported by experiment, from morphological facts.

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[1] Protoplasmamechanik, p. 122.
[2] Velten, Bot. Ztg., 1872, p. 651; de Vries, Bot. Ztg., 1885, p. 22.
[3] Königl. Akad. d. Wiss., Berlin, 1852.
[4] Protoplasmaströmung bei den Characeen, Jena, 1898, p. 13.

Velten[1] concluded that the streaming plasma always followed the path of least resistance, whereas Hörmann (l. c., p. 17) states that in elongated cells the current always follows the path of absolutely greatest resistance. Hörmann's remarks, however, would apply only if the friction were between a membrane and a fluid which did not wet it. In the plant-cell, the resistance to streaming is dependent solely upon (1) the viscosity of the streaming layers, which is unaffected by the direction of the streaming movement, and (2) upon the path followed. That the total resistance to a complete circuit around the long axis of a cell will be greater than around its short axis is self-evident, but the path of least resistance is that in which the passage across a certain space requires the least expenditure of energy. Now every bend or turn in the stream which is sufficiently sharp to produce eddy currents increases the resistance to flow, and hence, other things being equal, the path of least resistance will be that in which the current flows along a straight, or uniformly curved, path. A path parallel to the long axis of the cell will naturally be assumed when the cell is rectangular or flattened, and a spiral path fulfils the above conditions best when the cell is an elongated cylinder, as in *Chara* and *Nitella*. That the spiral direction of streaming in the latter case may be of biological utility is quite possible, just as may also be the spiral twisting of the cortical cells themselves, but teleological explanations afford no indication of causal relationship.

With regard to streaming in threads, it is important to remember that in thin ones the entire mass may appear to stream in a particular direction, whereas in thick ones showing streaming in opposite directions, the central portion is usually at rest.

SECTION 13. The Sources of Energy.

The direct agencies in producing streaming are probably physical in character, although the energy is without doubt ultimately derived from the chemical changes occurring in the protoplasm. Although we cannot at present refer the phenomenon to its immediate causes, this is no reason for evading the question by referring streaming to the domain of vital phenomena. All 'vital' phenomena are simply manifestations of the same elemental properties of matter, and of the same transformations of energy, with which the sciences of Chemistry and Physics make us familiar. The only difference is that in the case of organized structures these forces and properties often enter into complicated and interacting combinations, the precise nature of which is at present obscure. The physiologist must, however, hold in view the possibility that all 'vital' entities may ultimately be found reducible to simpler physical and chemical ones.

[1] Flora, 1873, p. 85.

It is easy to prove that streaming is not directly dependent upon supplies of radiant energy (thermal, photical, electrical) from without, for its initiation and maintenance[1], although indirectly it is dependent not only upon the maintenance of a certain temperature, but also, in the case of autotrophic plants, upon a supply of radiant energy in the form of light. The intensity of the illumination also apparently exercises a direct influence upon streaming, strong light retarding, and weak light often causing, a slight acceleration. The latter is most obvious in chlorophyllous cells, especially when the motion has become somewhat retarded in darkness. It may be due either to an increased supply of oxygen from the assimilation of internal or external supplies of carbon dioxide, or it may be owing to the slight rise of temperature which the absorption of light always causes, even when the dark heat rays are removed. Hence the acceleration is especially noticeable when preparations kept in darkness and at a low temperature for some time are illuminated.

A temperature lying within certain limits forms one of the essential conditions for streaming, the response being almost immediate. The velocity increases as the temperature rises, until the protoplasmic mechanism is injuriously affected. The increased velocity is in all cases partly due to the decreased viscosity which accompanies a rise of temperature, and in some cases may have practically no other origin. If the energy of streaming was directly derived from the absorption of heat from without, then, since the amount required is extremely small, the lowering of temperature by this cause would be quite imperceptible under ordinary circumstances. Evidence has, however, already been given against this possibility. Moreover, the production of heat by moderately active katabolism would much more than suffice to counterbalance any that might be consumed in this manner.

Both light and heat probably affect the protoplasmic mechanism as a whole, and hence influence cell-division, nutrition, growth, and katabolism, as well as streaming. As in the latter case, a part of the increased activity of growth consequent upon a moderate rise of temperature may be due to the decreased viscosity and hence increased motility of the protoplasm[2]. There can be no doubt, however, that the effect is largely an indirect one, in so far as it is due to the accelerating influence of the raised temperature upon metabolism in general.

Mechanical injuries, and indeed intense localized applications of energy in any form, often induce streaming in previously inactive cells. At the

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[1] For method and apparatus used, cf. Ewart, Journ. Linn. Soc., 1897, Vol. XXXIII, p. 123 (proof that the evolution of oxygen from certain coloured organisms is independent of external radiation).

[2] Diffusion and ferment-action are also accelerated.

same time they cause an increased respiratory activity[1] and an increased production of heat, a portion of the surplus energy apparently finding expression in the induced or accelerated streaming movements. The action is, however, an indirect one, and there is usually no graduated response in answer to stimuli of increasing intensity, the latter suddenly passing from a sub-minimal excitation to a nearly optimal one.

Streaming seems in all cases to be dependent upon katabolism of some kind or other, but need not necessarily be accompanied by aerobic respiration. That the ciliary movements of anaerobic bacteria continue in the absence of oxygen is well known, and in fact the movements of obligate anaerobes may cease in the presence of even small amounts of this gas. It is therefore possible that the cessation of streaming, produced in the cells of aerobic Phanerogams by the absence of oxygen, is merely due to a general effect upon the protoplasmic mechanism, and does not necessarily indicate a direct dependence of streaming upon aerobic metabolism. It is interesting in this connexion to notice that different plants exhibit varying powers of maintaining streaming in the temporary absence of oxygen.

In covered and ringed preparations of leaf-cells of *Elodea* kept in darkness, streaming ceases in about five minutes, but recommences almost at once when exposed to light, owing to the immediate production of oxygen by photosynthesis. After a prolonged arrest of streaming, however, partial asphyxiation ensues, and the chloroplastids temporarily lose the power of carbon dioxide assimilation, the oxygen necessary for the recommencement of streaming not being evolved until after the lapse of twenty minutes to an hour or more[2].

Even in the case of so aerobic a plant as *Elodea*, a very small amount of oxygen suffices for streaming. Thus I have previously shown (l.c., p. 566) that etiolated chloroplastids, which have at best a very weak power of photosynthesis, may produce sufficient oxygen to maintain slow streaming, and that the latter may continue under a partial pressure of oxygen which does not suffice for the turning green of etiolated chloroplastids. The precise minimal partial pressure of oxygen for streaming has been determined by Clarke to correspond to 1·2 mm. Hg. in the case of *Trianea*, 2·8 in that of *Urtica*, and 1·8 in *Elodea*[3]. Leaf-sections of *Vallisneria* are slightly more aerobic than leaves of *Elodea*, but otherwise behave similarly. Most species of *Chara*, on the other hand, seem to be partial anaerobes, while in the case of *Nitella* and *Chara foetida* the anaerobism is almost complete. This question is of special interest, and hence a more detailed account of it will be given.

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[1] Richards, Ann. of Bot., 1896, Vol. x, p. 531; 1897, Vol. xi.
[2] See Journ. Linn. Soc., 1896, Vol. xxxi, p. 403.
[3] Clarke, Ber. d. D. Bot. Ges., 1888, Vol. vi, p. 277.

SECTION 14. The Influence of Free Oxygen upon Streaming.

Corti[1] was the first to state that the presence of oxygen was an essential condition for streaming, and *Chara* was expressly included in this statement. I have already shown (l. c.) that streaming may continue in cell-preparations of *Chara* and *Nitella* for days or even weeks, though ringed with vaseline and kept in darkness. This was especially the case when only a thin ringing was applied, but streaming often continued for weeks in *Nitella*, even when the preparations were thickly ringed and immersed in oxygenless water kept in sealed bottles in absolute darkness. A few of the experiments upon which the above conclusions are based are given in detail beneath.

End-cells of *Chara*, axial cells of *Nitella*, leaves of *Elodea* in water, were covered, thinly ringed with vaseline, and kept in darkness at 15–18° C.

After three days.	Six days.	Nine days.	Ten days.
Nitella. Fairly slow rotation. Soon quickening in light, and active in quarter of an hour.	Slow streaming, active in fifteen to twenty minutes.	Slow creeping streaming, quickening in five minutes in light, fairly rapid in fifteen to thirty minutes.	As after nine days.
Chara. Slow streaming, active in five to ten minutes in light.	Slow streaming, moderately active in ten minutes, fully active in thirty minutes.	Barely perceptible streaming, still slow after five minutes. Moderately active after fifteen to thirty minutes in light.	As after nine days.
Elodea No streaming, commences in light in five minutes at base and margin of leaf, moderately rapid in quarter of an hour.	Streaming commences in five minutes; slow after ten minutes, active in ten to thirty minutes.	Few cells living, but neither streaming nor photosynthesis returns.	All leaf-cells dead.

Under the conditions given, minute traces of oxygen were able to diffuse in, although not in sufficient quantity to maintain the movement of strongly aerobic bacteria or infusoria. Occasional cells of *Chara* and *Nitella* cease to stream and die in from one to a few days under the above conditions. This may be due to some individual peculiarity, or to the metabolism of the cell being such as to temporarily demand relatively large supplies of free oxygen.

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[1] Quoted by Dutrochet and also by Meyen, Pflanzen-Physiologie, Bd. II, p. 224.

Carefully sealed preparations of end-cells of *Chara*, which were exposed to bright light for one minute daily, remaining living and exhibiting slow streaming until the thirtieth to thirty-sixth day, streaming ceasing on the thirty-sixth to fortieth day. Death is here, however, more the result of mal-nutrition than of a deficiency of oxygen. Slide preparations of *Chara* and *Nitella*, thinly ringed with boiled linseed oil, showed slow but quite perceptible streaming after twenty-eight days in darkness, the streaming quickening in ten to thirty minutes on re-exposure to light[1]. Farmer[2] states that streaming ceases or becomes extremely slow within half an hour, when cells of *Nitella* are kept in darkness in a current of hydrogen. If then exposed to light, streaming became active in one to two minutes, but on again darkening was nearly or quite arrested in five to seven minutes. According to Farmer, this shows that the oxygen produced by carbon dioxide assimilation in two minutes is used up by respiration in seven[3]. These conclusions are, however, hardly trustworthy, since slow streaming may be present after a whole day in darkness in a *stationary atmosphere* of pure hydrogen, although in a slow *current* of hydrogen streaming may be reduced to the same low ebb after one to three hours' darkness at 20° C.

It has previously been shown that the oxygen contained by a cell is evolved more rapidly in a *current* of H, than in an *atmosphere* of H or N, and much more rapidly than if immersed in oxygenless water[4]. This fact was overlooked by Farmer, and as a matter of fact fifteen to thirty minutes' daily exposure to bright light sufficed to maintain moderately active streaming, and a total daily exposure of three to five minutes maintained slow streaming in cells of *Chara* and *Nitella* enclosed in small air-tight glass cells containing at the outset 95 per cent. N and 5 per cent. CO_2.

Clarke (l. c.) found that streaming commenced in cells of *Nitella* at an oxygen pressure of from 1·2 to 2·8 mm. of mercury, i. e. in the presence of $\frac{1}{50}$ to $\frac{1}{100}$ of the normal amount of oxygen, but no mention is made of the time required for complete cessation, and in fact it is doubtful whether any such ever occurred.

In considering these observations, two fertile sources of error must be borne in mind. Firstly, when cells exhibiting very slow streaming are suddenly exposed to light and examined, the movement is usually missed

[1] After prolonged slow streaming all the larger granules, and many of the smaller ones, are deposited, leaving the streaming layer almost clear, and making slow streaming correspondingly difficult to distinguish immediately.

[2] Ann. of Bot., 1896, Vol. x, p. 288.

[3] Boussingault (Agron., Chim. agricole, &c., 1864, T. III, p. 378; 1868, T. IV, p. 286) and Holle (Flora, 1877, p. 187) state that chlorophyllous cells can decompose under optimal conditions from 15–30 times the amount of carbon dioxide that they exhale in the same time in darkness, and thus two minutes' photosynthesis would produce sufficient oxygen for 30–60 minutes' aerobic respiration.

[4] Ewart, Journ. Linn. Soc., 1896, p. 42.

at first, and hence seems to commence as the eye is focussed upon the cell. Secondly, the merest trace of certain gases (HCl, As H_3, SO_2) in the hydrogen employed will affect the accuracy of the results. Indeed, the injurious effect of currents of hydrogen on *Chara* and *Nitella* noted by certain observers is simply the result of the presence of poisonous impurities.

For example, if a current of hydrogen obtained from commercial zinc and pure dilute sulphuric acid is passed over darkened cells of *Chara* and *Nitella*, streaming ceases in one to two hours in the latter case, and in three to ten hours in the former.

If the tubes are clamped and the current stopped just before cessation, the streaming quickens somewhat, though still in darkness. The stoppage is probably partly due to the poisonous impurities in the hydrogen, and the recommencement or quickening to the presence of a trace of oxygen, for in deoxygenated hydrogen no such quickening occurs. In absolutely pure hydrogen, moreover, although streaming is reduced to a very low ebb, it does not entirely cease in these plants [1].

On the other hand, thickly ringed preparations of *Chara* and *Nitella* immersed in oxygenless water in darkness cease to show streaming in two to four days, and die in from three to five. This is, however, not so much due to the absence of oxygen as to the accumulation of the products of intramolecular respiration (CO_2, and possibly traces of organic acids or alcohol). In thinly ringed preparations kept in air the carbon dioxide and alcohol diffuse outwards, and hence the cells remain living for weeks in darkness, whereas if immersed in carbon dioxide or in air saturated with alcohol vapour this cannot occur, and the cells die in two to five days. Cells of *Nitella* and *Chara* cease to show streaming within fifteen minutes in an atmosphere containing 95 per cent. carbon dioxide and 5 per cent. oxygen, and are killed in less than an hour even if illuminated.

It is owing to the facts just mentioned that Ritter [2] has obtained contradictory results to my own, and to the later one by Kühne [3], who found that streaming may continue in *Nitella* for a month in the absence of free oxygen, and concluded that this is due to the presence of an internal store of oxygen. Ritter, on the other hand, states that streaming ceases in four days in *Chara stelligera*, and in two to three days in *Nitella*, the cells remaining living a day longer.

There are, therefore, almost as many contradictory results as there have been investigators, and as instances of the caution necessary in

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[1] The hydrogen used for my own test experiments was obtained from nearly pure zinc and pure sulphuric acid, and was purified by passing through solutions of Na_2CO_3, $AgNO_3$, KHO and alkaline pyrogallol, all in U tubes containing pumice-stone. The surface of acid in the generator was covered with liquid paraffin, and all connexions, as well as the entire purifying apparatus, were placed under water covered by liquid paraffin.

[2] Flora, LXXXVI, 1899, pp. 329–60. [3] Zeitschr. f. Biol., 1897, Bd. XXXV, p. 43; 1898, p. 1.

investigations of this kind, and of the importance of securing absolute purity in the gases employed, it may be mentioned that Lopriore[1] came to the conclusion that streaming cannot be stopped in cells of *Tradescantia* by pure hydrogen, while Demoor[2] has stated that streaming continues in nitrous oxide (N_2O) and is even accelerated. Samassa[3] has, however, shown that the latter statement is erroneous, and my own observations, as well as those of Kühne[4] and Demoor (l. c., p. 32), conclusively prove that in an atmosphere of pure hydrogen streaming ceases in non-illuminated hairs of *Tradescantia* within from fifteen minutes to two or three hours, according to the temperature, and also the age and condition of the cells. The contradictory results with regard to the influence of *pure* oxygen are due to the fact that it retards streaming in facultative anaerobes, and temporarily accelerates it in strongly aerobic ones only when previously slow, the accelerating influence being especially marked in non-assimilating cells with cuticularized walls.

In the case of *Chara* and *Nitella*, the problem is to remove every trace of free oxygen with as little disturbance as possible, and to prevent any injurious accumulation of the products of intramolecular respiration. This can be done by placing a healthy filament of *Chara* or *Nitella* in an open tube containing cold boiled

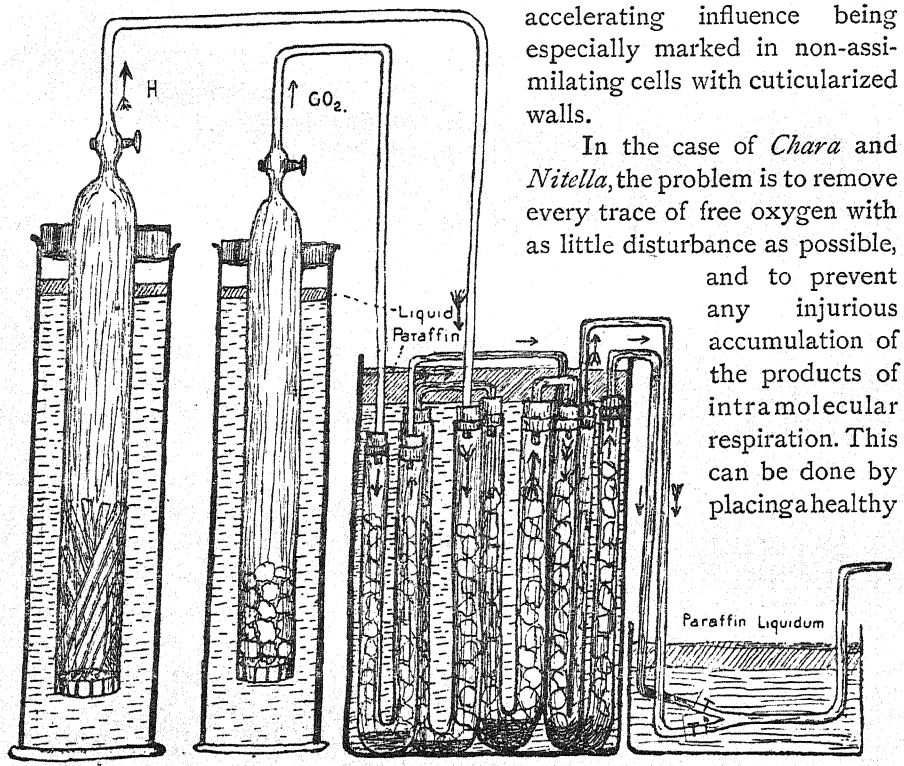

FIG. 6. Apparatus for obtaining pure hydrogen and pure CO_2 free from all oxygen (one-tenth natural size).

[1] Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 531.
[2] Archives d. Biologie I., 1894, XIII, p. 163.
[3] Bot. Ztg., 1898, p. 344.
[4] Unters. über das Protoplasma, &c., 1864, p. 105.

water taken from the culture-vessel. The tube was placed in a bottle containing a solution of pyrogallol and caustic potash (Fig. 7), which is kept immersed under water. Pure hydrogen (Fig. 6) is then passed through as shown, until the air is all displaced. The entry-tube is then clamped and the vessel exhausted by a Sprengel pump. Hydrogen is again passed in, and after one or two repetitions, the exit- and entry-tubes are drawn out and sealed. The whole is then covered with black cloth and placed in a dark cupboard. The only possibility of error here is that the water might have absorbed oxygen during cooling, but it could only retain the merest fraction of this. Moreover, the water in the tubes was frequently tested by means of reduced indigo solution immediately on opening, and always with negative result, even if opened the day after sealing.

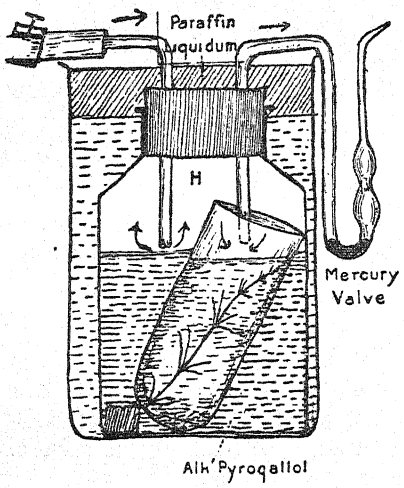

FIG. 7. Apparatus for testing the anaerobism of *Chara* and *Nitella* (two-thirds natural size).

Experiments conducted in this manner succeed with sufficient frequency to prove conclusively that healthy plants of *Chara foetida, Nitella translucens, N. flexilis*, and to a less extent *Nitella syncarpa, Chara gracilis, C. flexilis*, and *C. stelligera* may continue at temperatures of from 15° C. to 18° C. to show slow streaming for from one to several weeks in the entire absence of oxygen. In a few cases small new side sprouts were formed during the first two or three weeks, but not after this. Many filaments of the first three plants were still living after six weeks, and exhibited slow creeping streaming immediately on examination, but in no case did any remain living for longer than eight weeks. The ultimate death is not due to the absence of oxygen, but to mal-nutrition, for darkened parts of *Chara* and *Nitella*, even if attached to the parent plant, die within two months, although supplied with free oxygen[1].

The cells might remain living longer were they provided with appropriate food and the medium kept sterile, but if they are placed in nutrient solutions containing sugar, glycerine, or asparagin, anaerobic bacteria develop whose by-products rapidly injure the filaments. The oosperms can be sterilized and sown in sterile media, but unfortunately they refuse to

[1] See Ewart, Journ. Linn. Soc., 1896, Vol. XXXI, p. 564; cf. also Ritter, Flora, 1899, LXXXVII, p. 329.

germinate in the absence of oxygen. Hence it still remains to be decided whether the anaerobiosis of *Chara* and *Nitella* is always merely temporary and facultative, or whether these plants, under special conditions of nutrition and environment, can be converted into completely anaerobic saprophytes. An interesting point is that in several cases cells remained living for some time on re-exposure to light and air, especially if fed with dilute glycerine, although their relatively more aerobic chloroplastids showed signs of fatal injury, producing no starch, and ultimately becoming completely bleached.

In other cases, the admission of air causes merely a slight temporary quickening of streaming, soon followed by its complete cessation. Apparently the entrance of free oxygen so disturbs the anaerobic metabolic equilibrium as to cause rapid death, probably much in the same way that free oxygen causes the death of obligate anaerobes.

That slow streaming does actually continue during the whole time that oxygen is absent, and does not merely commence at the moment of examination, is easily proved by arranging so that the cells can be observed under a low power before oxygen is admitted, and since the chloroplastids have temporarily or permanently lost the power of CO_2-assimilation, the short exposure to light during examination does not cause any production of oxygen by photosynthesis.

There is only one other possibility to consider, which is, whether the cells of *Chara* and *Nitella* may contain a store of occluded oxygen, or of oxygen held in a state of loose chemical combination, which could be utilized for the maintenance of the minimal amount of aerobic respiration necessary to preserve the vitality of an aerobe. It has already been shown[1] that certain bacteria do actually possess a pigment which has the power of occluding oxygen, and that they are able to respire for a short time at the expense of this oxygen in the absence of any external supply. The fact that the absorbent substance is coloured is a mere accident, and hence *Chara* and *Nitella* might easily have a similar power of storing or occluding oxygen, although they produce no such pigments as are formed by these bacteria.

That neither the calcareous incrustation of *Chara* nor the cell-wall has any such property is easily proved by the use of test-bacteria, and by means of solutions of reduced indigo-carmine (l. c., p. 126). Similarly, the expressed sap contains normally only a small trace of dissolved oxygen, and after the cells have been kept in darkness and in pure hydrogen for an hour or two, this trace entirely disappears. The latter can be shown by placing cells over a gas chamber in the usual manner, but with a strip of glass crossing underneath them. On applying pressure the cell bursts,

[1] Ewart, Journ. Linn. Soc., 1897, Vol. XXXIII, p. 123.

and the escaping sap neither produces any colouration in reduced indigo-solution, nor excites any movement in motile aerobic bacteria.

Nor does the plasma contain any occluded oxygen, and the amount of dissolved oxygen it holds is relatively small, even in the immediate neighbourhood of actively assimilating chloroplastids. The oxygen produced by them is, in fact, liberated almost immediately upon the external surface, and hence it arises that streaming may ultimately cease in the more aerobic species of *Chara* (*C. flexilis*, *C. stelligera*) as well as in strips of leaf-cells of *Elodea* and *Vallisneria* after prolonged immersal in a stream of hydrogen containing a little carbon dioxide, even though exposed to continuous illumination.

It is certain, therefore, that several species of *Chara* and *Nitella* are facultative anaerobes, and it is interesting to notice that within certain limits the previous, as well as the immediate external conditions, exercise an important influence upon the degree of anaerobism. Thus this peculiarity is more marked in plants from muddy, stagnant water, than in those from clear well-aerated habitats. This not only applies to different species, but also in a less degree to different individuals of the same species. Moreover, the plants are more aerobic at higher temperatures (25 to 30° C.) than at lower ones (15 to 20° C.). The facultative anaerobism of *Chara* and *Nitella* is to be regarded as a secondary modification produced by the exigencies of their surroundings, and a small fraction of the energy of anaerobic respiration suffices for the maintenance of slow streaming.

SECTION 15. **Influence of Electrolytic Oxygen.**

The action is similar to that of ordinary oxygen, except that an energetic oxidizing action is exercised at the moment of liberation. This may suffice to produce a brownish colouration in the cell-wall, or to decolorize coloured cell-sap, or to kill the protoplasm. With weak currents, however, no pronounced injurious effect is at first exercised. Thus, if leaves of *Elodea* or leaf-sections of *Vallisneria* are laid across platinum electrodes, covered, ringed, kept in darkness until streaming has ceased, and then traversed by a weak constant current for one to a few minutes, on lifting the dark cover streaming will usually be seen over the positive electrodes, but will not appear over the rest of the leaf until after fifteen to thirty minutes, if the preparations have been kept two to three hours in darkness, so as to temporarily inhibit the resumption of photosynthesis. Similarly, if cells of *Chara* or *Nitella* are used, streaming may be distinctly more rapid at the end lying near to the positive electrode, although a strength of current sufficient to produce distinct electrolysis usually acts as a supra-maximal stimulus to streaming in these plants. Sufficiently resistant cells can usually be found after a few trials, if a current of 2 to 3

volts is used, and the quantity passing through the cell decreased by interposing a long filament and surrounding it with water.

SECTION 16. **Chemical Changes connected with Streaming.**

Beyond the changes due to the accompanying aerobic or anaerobic respiration, no special chemical changes seem to be connected with the existence and maintenance of streaming. Czapek[1] states that in the apical meristems of curving roots reducing substances appear to increase, while the oxidases decrease. This is probably the result of increased katabolism, but no changes of this kind seem to take place in cells in which secondary streaming has been induced by stimulation, provided they are well aerated. If, however, the cells are insufficiently aerated and kept in semi-darkness, a slightly increased acidity of the sap (organic acids), or even the appearance of substances which have the power of reducing alkaline solutions of silver salts may result. The same phenomenon is, however, shown by non-streaming cells, and hence it has no direct connexion with streaming.

SECTION 17. **Electrical and Magnetic Properties of the Cell.**

Hitherto but little experimental work has been attempted in this direction, and, in spite of its importance, it rests almost entirely on theoretical and frequently incorrect assumptions. It is, for example, essential to know whether or not the existence of streaming is connected with the presence of electrical currents in the cell, as Velten suggests[2].

Reinke, however, states that freely suspended streaming cells retain any position in which they may be placed in a magnetic field, and hence concludes that no electrical currents circulate in them. Even were Reinke's facts correct, his conclusions would not be a necessary consequence of them. It is easy, for example, to arrange two similar solenoids with interlacing coils and opposed currents so that they shall exhibit no external electro-magnetic properties. Moreover, as we shall see later, *the cellulose wall is distinctly, though weakly, magnetic*, and hence a pronounced directive action is usually exercised upon elongated cells freely suspended in a magnetic field. Indeed, from a physical point of view, it appeared highly improbable that all plant-cells possessed exactly the same magnetic permeability as water, as the absence of all directive action in a magnetic field (Reinke) would indicate. Reinke suspended plant-cells in hanging drops of water, and used as his electro-magnet a hollow bar 200 mm. long and 40 mm. diam., covered by a 17 mm. thick coil of wire charged by four Bunsen cells. The

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[1] Ber. d. D. Bot. Ges., 1897, Vol. XV, p. 516.

[2] Velten, Flora, 1873, p. 122. First put forward by Becquerel, Ann. sci. nat., 1838, ii. sér., T. IX, p. 68.

end of a smaller magnet brought near to the object formed the other pole. In my own experiments the electro-magnet used consisted of two parallel arms placed horizontally, and with pointed pole-pieces, which could be adjusted across the stage of a microscope so as to be any distance apart, from a millimetre upwards. Each iron core was 4 cm. diameter, its height was 30 cm., and the diameter across the coils was 15 cm. A current of 12 volts was used to charge the coils, which gave 22 amperes against a resistance of about $\frac{1}{2}$ an ohm.

Observations upon the directive action of a magnetic field were carried out by suspending plant-cells and other objects in still moist air between the poles of the electro-magnet by means of fibres of unspun silk. With large objects, a strand of six to ten untwisted fibres may be used. The manipulation is naturally somewhat difficult, since the object must lie horizontally when suspended, but the copper loops and paper stirrups used by Faraday are unsuitable, in the first case owing to the disturbing effect of the currents induced at each movement, and in the second one owing to the fact that paper is paramagnetic.

Experimenting in this manner with suspended living cells of *Chara* and *Nitella*, it was at once seen that they swing so as to set their long axes parallel to the lines of force in the field. The same was shown when suspended in water, although the movement was slower, owing to the greater inertia of the water. Either end was presented indifferently to either pole, and hence the movement is not the result of the existence of galvanic currents in the cell, but is due to the average magnetic permeability of the different constituents of the plant-cell being greater than that of air and of water. Similar results were given by strips of leaf-cells of *Elodea* and *Vallisneria*, by leaves of the onion, and more strongly by peduncles of *Primula*, *Narcissus*, and *Tulipa*, as well as by the petioles of various leaves and the stems and leaves of grasses. All these objects were as strongly paramagnetic when dead, and when dry, as when living and moist. The phenomenon is, therefore, a purely physical one, but the results obtained are somewhat surprising, since Faraday[1] explicitly states that sugar, starch, gum-arabic, wood, dried and fresh mutton and beef, apples, bread, fresh and dry blood, leaves, &c., are all diamagnetic, while Reinke obtained negative results with plant-cells. A possible explanation of the latter's results lies in the fact that no directive action is exercised upon a small object placed in a large uniform field, since in all positions it is traversed by equal numbers of tubes of force. If, however, pointed pole-pieces are used, or if the object is brought towards the periphery of the field, it will set itself at right angles to, or parallel to, the lines of force, according to whether it is diamagnetic or paramagnetic.

[1] Experimental Researches on Electricity, 1855, Vol. III, p. 35.

Faraday's contradictory observations are not quite so easily disposed of, and hence it seemed of interest to repeat and extend or overthrow the somewhat scanty observations made by him upon plant and animal substances. It may at once be mentioned that all external contamination with iron was avoided throughout. The magnetic permeability of a compound material is naturally the algebraic sum of the magnetic permeabilities of the separate constituents, multiplied by the fractional amounts of them present. An estimate of the magnetic permeability of a substance can best be made by noting the directive action of a magnetic field upon it when suspended in liquids of known permeability. Air is very feebly diamagnetic, and hence a body, which is paramagnetic in air, will usually be paramagnetic in a vacuum also; alcohol is, however, much more strongly diamagnetic than air, and water still more so. The following table gives the results obtained in these media:—

Substance [1].	In air.	In alcohol.	In water.
Cellulose	Strongly paramagnetic	Strongly paramagnetic	Very strongly paramagnetic
Pure cotton wool			
Ashless filter-paper (0·028 per cent. of ash. No iron)			
Filter paper (saturated with water)	Fairly strongly paramagnetic	Strongly paramagnetic	Strongly paramagnetic
Wood and cork (saturated with water)			
Dry wood (pine, fir, mahogany, oak, ash, elm)	Strongly to moderately paramagnetic	Strongly paramagnetic	Strongly paramagnetic
Cuticle (thin)	Weakly paramagnetic	Paramagnetic	Paramagnetic
Cuticle (thick)	Feebly diamagnetic	Paramagnetic	Paramagnetic
Starch (dry)	Weakly diamagnetic	Doubtful	Feebly paramagnetic
Gum-arabic (dry)			
Glucose	Weakly diamagnetic	Very feebly paramagnetic	Feebly paramagnetic
Cane sugar (pure)			
Cane sugar (caramelized at 150° C.)			
Normal egg-albumin (82 per cent. water)	Diamagnetic	Feebly paramagnetic	Paramagnetic
Coagulated egg-albumin (82 per cent. water)			
Dry egg-albumin	Paramagnetic	Fairly strongly paramagnetic	Strongly paramagnetic
Olive oil	Moderately strongly paramagnetic	Very feebly paramagnetic	Weakly paramagnetic
Dried beef and mutton (lean)			
Dried sheep's blood [2]—			
Pieces from bottom (more haemoglobin)	Weakly diamagnetic	Neutral	Very faintly paramagnetic
Pieces from surface (more albumin)	Paramagnetic	Paramagnetic	Paramagnetic
Fresh blood	Moderately strongly diamagnetic	Feebly diamagnetic	Faintly paramagnetic
Oxyhaemoglobin [3] (pure, dry)	Weakly diamagnetic	Feebly paramagnetic	Weakly paramagnetic
Fibrin (pure, dry)	Moderately strongly diamagnetic	Weakly paramagnetic	Weakly paramagnetic

[1] Solids were cut or cast into short rods; liquids or solids acted on by the medium were placed in thin, very feebly paramagnetic glass tubes.

[2] Blood contains barely 0·2 per cent. of fibrin, and nearly twice as much haemoglobin (13·5 per cent.) as albumin 7·6 per cent., the fats, salts, and extractives totalling less than 1 per cent.

[3] I have since found that the same result has been obtained by Gamgee (Proc. Royal Soc., 1901, Vol. LXVIII, p. 503) in the case of both oxyhaemoglobin and CO-haemoglobin.

Substance.	In air.	In alcohol.	In water.
Serum albumin (pure, dry)	Strongly paramagnetic	Strongly paramagnetic	Very strongly paramagnetic
Keratin (dry from hair)	Moderately strongly paramagnetic	Paramagnetic	Paramagnetic
Gelatin (dry)	Weakly paramagnetic	Paramagnetic	Strongly paramagnetic
Gelatin (saturated with water)	Very feebly diamagnetic	Neutral	Feebly paramagnetic
Chlorophyll [1]—			
(*a*) Dry alcoholic extract	Fairly strongly paramagnetic	Strongly paramagnetic	Strongly paramagnetic
(*b*) After extraction with ether	Strongly paramagnetic	Strongly paramagnetic	Strongly paramagnetic
(*c*) Dried ether extract	Weakly diamagnetic	Almost neutral	Feebly paramagnetic

It is interesting to notice that cellulose, starch, gum-arabic, glucose, and cane sugar form a series of substances with progressively decreasing magnetic permeability, and the same applies to the series, serum-albumin, egg-albumin, keratin, gelatin, haemoglobin, fibrin, myosin.

Chlorophyll, which contains no iron, is paramagnetic, whereas haemoglobin, which contains 0·4 per cent. by weight of iron, is diamagnetic. The oxides, and all ordinary salts of iron, are paramagnetic in air ($Fe\,Cl_2$, $Fe_2\,Cl_6$, $Fe_2\,SO_4$, $Fe_2\,3\,SO_4$, $Fe\,CO_3$, $Fe_3\,PO_4$, $Fe\,3\,NO_3$, $Fe_4 3\,(Fe\,C_6\,N_6)$, whereas salts containing the iron in the form of an acid ($K_4\,Fe\,C_6\,N_6$: $K_3\,FeC_6\,N_6$) are diamagnetic. Hence the iron of haemoglobin is not present in basic form, but occurs in the form of an electro-negative radicle as in the above cyanogen compounds. Under the action of acids and alkalies haemoglobin readily splits up into haematin and an albuminous substance. Now Gamgee has recently shown that haematin is paramagnetic, and hence, apparently, contains the iron in basic form, and if the albumin derivative is also paramagnetic (see previous table), we have the curious circumstance of a diamagnetic substance being resolved (in the presence of oxygen) into two paramagnetic ones. Plants, as a whole, are paramagnetic, and this applies even to parts rendered chlorotic by growth in a culture-solution free from iron, but tissues rich in water and with little cellulose, leaves packed with starch, and etiolated leaves in some cases (onions, &c.) may be feebly diamagnetic, but are always paramagnetic when dried. Faraday's hasty, incorrect generalization was probably the result of examining parts of plants which were in an abnormal condition. This is, however, of little importance, as compared with the fact that plants con-

[1] Leaves were dropped in boiling water, triturated, treated with cold (1) ether, (2) 50 per cent. alcohol, (3) 75 per cent. alcohol, and then extracted with warm absolute alcohol, filtered in darkness, the filtrate being evaporated to dryness on a water bath. This residue (*a*) was then extracted with ether to remove fats and oils (*c*) and the residue (*b*) again dried and tested.

tain substances which have different magnetic properties, and though all are attracted (paramagnetic) when in water, the force of attraction differs greatly. Hence it follows that, given a sufficiently powerful field, some action, whether retarding, accelerating, or directive, must be exercised not only upon growth, but also upon streaming. Negative results simply indicate that the field is not powerful enough to overcome or modify the other forces at work in the cell, and hence is unable to produce an externally perceptible result. The influence of magnetic forces on growth must be left for future solution, but the problem as to their effect on streaming is more susceptible to attack, and has indeed already been answered in the negative by Reinke (l. c.) in the case of *Chara*.

SECTION 18. **Influence of Magnetic Forces on Streaming.**

No change in the plane of rotation, in the position of the indifferent line, or in the direction of streaming was ever produced, however strong the field might be. This is hardly surprising, when we consider that gravity exercises no directive action on streaming, and that the magnetic forces acting on the cell-constituents were always very much weaker than that of gravity. The latter does, however, slightly influence the velocity of streaming in large cells, but in a magnetic field, purely negative results were at first obtained, the long axes of the cells being parallel to the lines of force, and the pole-pieces two centimetres apart. Thus :—

	Off[1].	On.	Off.	On.	Off.	On.	Off.
Vallisneria	63	62	61	62	62	63	61
Chara	25·2	25	24·6	24·8	25	24·5	24·8

Similar results were obtained with *Nitella* and *Elodea*, and little or no effect was exercised even when the action was more prolonged.

	Off.	On.	After 10 minutes.	After 20 minutes.	After 30 minutes.	Off.
Chara	23·3	23	23·5	23·4	23·2	22·5
	22	22	23·2	23·8	24·6	24
	14·3	15·1	14·7	14·3	14·8	13·5
Vallisneria	48	48·5	48·3	48	48·2	48·5
	50·8	49·7	49	47·5	47·4	47·6

In the last case the quickening is possibly the result of a change of *tempo* of internal origin, since it persists when the field is destroyed.

[1] Off = no field, on = full field. The numbers are averages of from 6 to 10 observations of the metronome beats made while the stream crosses a measured space.

If, however, the pole-pieces are placed 5 to 10 mm. apart, and the cells are arranged so that the direction of streaming cuts the lines of force at right angles, distinct effects are produced. The ultimate effect is always to retard streaming, although curiously enough the first effect may be either to produce a slight acceleration or a slight retardation.

	Off.	On.	After 10 minutes.	After 20 minutes.	Off.	After 10 minutes.	After 1 hour.
Chara	25·8 15·6	26 17	31·3 18·3	32 25·5	32·5 28	28·8	28 16·8 Next day, 15·9

In another case, after one hour streaming was slow and irregular and ultimately ceased, the cell dying. This happened frequently after very long exposures, not only with *Chara*, but also with *Nitella*, *Elodea*, and *Vallisneria*, provided that the direction of streaming cut the lines of force at right angles, or nearly so.

	Off.	On.	Off.	
Vallisneria	(*a*) 23	23·5	23·6	at right angles to lines of force.
	(*b*) 55	54	53·6	
	(*c*) 48	48·5	48·1	parallel to

	Off.	On.	After 3 minutes.	10 minutes.	15 minutes.	Off.	After 10 minutes.	After 30 minutes.
Time experiment	48·5	48	48·6	61·2	66·4	66	52·6	52·4

The passage of the streaming plasma across the lines of force in the field causes a weak constant current to pass around the short axis of the cell, and since the medium is not homogeneous, a slight electrolytic effect will be exercised at various points. The velocity of streaming is relatively extremely slow (1 to 3 mm. per min.), and hence the current is proportionately weak, but Hörmann[1] has shown that a current of 0·000,000,030,884 ampère suffices to cause a temporary stoppage in a highly excitable cell of *Nitella* of diameter 610 μ. Moreover, the excitability is increased by previous electrical excitation, and hence it is easy to understand the retarding effect produced by prolonged exposure in a magnetic field under the

[1] Protoplasmaströmung bei den Characeen, Jena, 1898, p. 65.

conditions given. This retardation is best shown in *Chara* and *Nitella*, which have large and sensitive cells, but is shown even in leaf-cells of *Vallisneria*, *Elodea*, and in hair-cells of *Tradescantia* and *Trianea*[1] when the pole-pieces are close together and the magnets fully charged.

A more marked percentage retardation is shown when streaming is rapid (viz. at 30° C.) than when it is slow (viz. at 10° C.). This is probably because of the increased current, the latter being directly proportional to the rapidity of flow across the field. If the action is not too prolonged, the original *tempo* is usually resumed after a longer or shorter period of recovery, but otherwise may be slower than before, and in some cases after prolonged exposure (half to one hour) a progressive retardation ensues, the cells ultimately dying. This is apparently not the result of any operative injury, for outside the field similarly treated cells remain living for an indefinite length of time. Sometimes a temporary or permanent localized retardation is exhibited over certain areas of the cell, although streaming is nearly normal in other parts. This points to a localized electrolytic action.

At each make and break of the field a current of very short duration tends to pass around the cell, but it is so momentary that it never suffices to produce a shock-stoppage. Very weak currents may sometimes at first accelerate slow streaming, although stronger ones always retard. Hence possibly arises the occasional slight acceleration seen on making the field. The current produced at break is stronger than at make, and hence it seemed possible that by summating the effects, a marked result might be produced. Making and breaking the field 1,200 times in ten minutes produced no perceptible effect upon the movement of Infusoria and Bacteria, although a slight retardation could usually be seen in *Chara*, *Nitella*, and *Vallisneria*, especially when 2,000 makes and breaks were made in ten minutes, or 3,000 in fifteen, and when the long axes crossed the lines of force at right angles. This may possibly be because the current passing round the short axis of the cell has a shorter path than round a long axis, and hence encounters less resistance.

Like Reinke, the author was unable to detect any movements or changes of position of streaming threads in plant-cells, which could be referred to the direct action of the magnetic forces. Since, however, a feeble directive attractive force is actually exercised upon them when in water, it is only a question of obtaining a sufficiently powerful field to cause them either to break or to set themselves along particular lines. It must be remembered, however, that in thin threads, as the diameter decreases, the surface-tension pressure increases, and hence also the relative rigidity of the thread.

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[1] The objects were placed on strips of glass four millimetres broad, and examined in water.

SECTION 19. The Influence of Magnetic Forces on freely motile Organisms.

Both aerobic and anaerobic motile Bacteria, ciliate and flagellate Infusoria, as well as the spermatozoids of a few plants, were used. Even the strongest field exercised no perceptible directive influence, nor was the velocity of movement affected by the entry or exit of the field. This is, however, hardly surprising, for the propulsive force necessary to overcome the resistance of the water must be considerable as compared with the restraining and directive action exercised by the field. Similarly, no perceptible retardation could be seen after actively motile Infusoria and Bacteria had been moving about in all directions in a strong field for fifteen to thirty minutes.

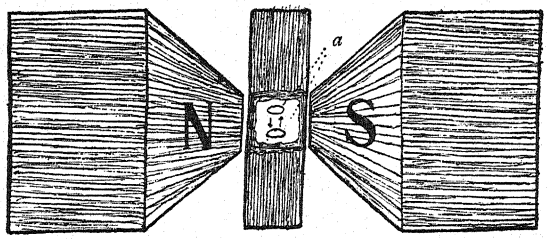

FIG. 8. Ringed preparation of motile organisms between the pole-pieces of an electro-magnet. *a* = air-bubbles.

If, however, aerobic forms are placed under a ringed cover-slip, as in the figure, the organisms pass to and fro from one air-bubble to the other across the lines of force, and hence are subjected to internal electrical currents altering with each change in the direction of movement. These produce in ten to forty minutes a retardation which may amount to a quarter to three-quarters of the average original velocity. If the air-bubbles are large and the number of organisms limited, an optimal supply of oxygen is assured for two or three hours, and on removing the field the velocity often increases again in half to one hour. In other cases the retardation is permanent, and on lifting the cover-slip no acceleration occurs. These results are best shown by large and small flagellate infusoria.

When the period of swarming is limited, as in the sperms of the fern, *Chara* and *Vaucheria*, these seem to come to rest sooner in a strong field than they would otherwise have done, the difference often amounting to as much as a quarter to one hour. Non-motile elongated bacillus-rods frequently swing slightly or show a tendency to place their long axes parallel to the lines of force in a strong magnetic field. Even slowly moving forms, however, are able to overcome this directive action, and hence to move in all directions, but if they are allowed to come to rest [1] in the field, around the periphery of the latter though not at the centre, it can frequently be noticed that the long axes of the greater number make angles of from 0 to 45° with the lines of force. The organisms are obviously paramagnetic in water.

[1] In a hanging drop and also in ringed preparations. Most Infusoria burst shortly after all the oxygen has been exhausted.

CHAPTER III

PHYSIOLOGY OF STREAMING MOVEMENTS

SECTION 20. General.

WE are here concerned with the connexions between streaming movements in general and the other vital functions, as well as with those phenomena of protoplasmic movement which we are unable at present to directly refer to simple physical and chemical causes. Instead, therefore, of adopting the analytical treatment, the phenomena in question will be discussed from a purely experimental and empirical point of view. It must, moreover, always be borne in mind that obscure internal stimuli or internal changes which can neither be predicted, estimated, or controlled may frequently modify the velocity of streaming, and sometimes to such an extent as to vitiate the accuracy of results obtained by special experimentation. Thus a stimulus to streaming, when once applied, may cause little or no effect to be exercised by stimuli which markedly influence normal unstimulated cells. Hence, in comparative experiments, it is of the utmost importance that the material used should have been kept for some time previously under uniformly and homogeneously optimal conditions, and should be at approximately the same stage of development.

Among the internal influences which affect streaming, those radiating from the nucleus are undoubtedly of great importance, although they appear to act mainly in an indirect manner, and not to exercise any directly appreciable controlling influence. Streaming is always dependent upon katabolism of some kind or other, although this need not necessarily take the form of oxygen-respiration. The amount of dependence upon other functions, however, varies, and the physiological importance of streaming may alter according to external circumstances.

Certain streaming movements of the protoplasm are not directly connected with any vital functions whatever, but have a purely physical origin. This is the case with the movements in mass of the protoplasm which commonly occur in the mycelial filaments of many Fungi[1]. These may continue or may be induced for a short time in the absence of oxygen, but

[1] Cf. J. C. Arthur, Ann. of Bot., 1897, Vol. XI, p. 491.

the power is soon lost owing to the protoplasm of these strongly aerobic fungi being soon fatally affected and the cells hence losing their turgidity under such conditions.

The death of the protoplasm causes the cessation of the changes in the distribution of water and in the osmotic pressure to which the movements are due. A direct dependence upon oxygen-respiration would certainly have been inferred from these facts had not the precise causation of the movement been known. Similarly, it is not impossible that many protoplasmic movements which are apparently vital in origin may not really be so. For example, protoplasmic movement in *Chara*, *Nitella*, and in motile anaerobic bacteria is largely or entirely independent of oxygen respiration, and although we may assume that it is directly connected with respiratory katabolism of some kind or other, the connexion might equally well be an indirect or even accidental one. Dormant life without respiration is possible in the case of many dry seeds and mosses, and similarly the power of movement may be temporarily or even permanently inhibited without vitality being impaired.

SECTION 21. **Relation between Streaming and Assimilation.**

Streaming is always absent from very young cells in which assimilation is active, and also from cells loaded with food-materials, although it may appear as these are emptied. There is, however, no reason for assuming a direct connexion between the two functions, and similarly with regard to *photosynthesis* only indirect relationships appear to exist. In the absence of free oxygen, however, streaming becomes dependent upon photosynthesis in chlorophyllous aerobes. For example, if leaf-sections of *Vallisneria* or leaves of *Elodea* are mounted in water, ringed with vaseline-paraffin mixture, and kept in darkness, streaming usually soon ceases, but recommences again on exposure to light. If the preparations are kept in darkness for from eight to fourteen hours, streaming may not recommence on exposure to light until after half an hour or more, and even after two hours may be slow or barely perceptible[1]; although similar preparations to which free oxygen is admitted show active streaming in from thirty seconds to five minutes. During this period of half to two hours the function of photosynthesis is temporarily in abeyance, but a facultative power of streaming is usually present the whole time. If preparations are alternately illuminated for five to ten minutes and darkened for a few hours, it will be found that frequently streaming continues for a longer time in darkness than it did after the second exposure, the cells evidently accommodating themselves to a certain extent to the new conditions.

If a closed cell-preparation of *Elodea* and *Vallisneria* is warmed to

[1] Similar observations have been made by F. Darwin.

46° C. streaming ceases in five to ten minutes, and at 42° C. in fifteen to thirty minutes, in both cases recommencing in five to fifteen minutes at 20° C. Preparations kept at 40° C. to 42° C. for an hour may show no recommencement of streaming, however long they are exposed to light, although streaming may reappear if oxygen is admitted, and may or may not continue when the preparations are closed again, according to whether the power of photosynthesis has been permanently or only temporarily lost. A rise of temperature accelerates streaming and respiration, but above certain limits retards or inhibits photosynthesis. Hence in closed cell-preparations, a rise of temperature to over 40° C. at first accelerates streaming, which later slows and ultimately ceases in most cases. It may then recommence some time after the temperature has been lowered to 20° C. if the illumination is maintained, while, *if free oxygen is admitted*, it begins at once, or almost at once, in all cells where it was previously present.

SECTION 22. **Relation between Growth and Streaming.**

Very young growing cells exhibit for some time after division has ceased, only very slow and irregular protoplasmic movements. It is only as the cell grows older that active streaming becomes possible, and regular rotation begins only when the cell is fully grown or nearly so. Hence a certain antagonism seems to exist between the two functions, although the growth of young cells in which 'secondary streaming' has been induced by artificial excitation does not seem to be retarded in any way.

In the case of large and especially of long cells (*Chara*, *Nitella*, midrib cells of *Elodea*, &c.) the continuance of streaming seems to form an essential condition of existence. When once commenced, it never ceases under normal conditions, and it cannot be stopped permanently, or for at all prolonged periods of time, without injuriously or fatally affecting the vitality of the cell. This is probably because in such cells the circulation of the protoplasm is an important factor in regulating its nutrition, and hence becomes an ingrained habit. External growth is, however, always the direct result of the activity of the non-streaming ectoplasm, the rotating endoplasm securing a rapid transmission of food-materials from one part to another. Hence even where 'primary' streaming exists there is no direct but frequently a marked indirect connexion between it and external growth.

SECTION 23. **The Influence of the Nucleus on Protoplasmic Movement.**

The retention of the power of movement by non-nucleated fragments of animal cells is a well-established fact. Thus Hofer[1] has shown that under such conditions the contractile vacuoles of Infusoria may continue to

[1] Exp. Unters. über den Einfluss d. Kernes auf das Protoplasma, 1889, p. 486.

pulsate, and that non-nucleated fragments of Amoebae obtained by artificial fission may continue to exhibit amoeboid and streaming movements as soon as the shock of the operation has passed away. Similarly, ciliary movements may continue in non-nucleated fragments of columnar epithelial cells, of swarm-spores, and of ciliate Infusoria[1]. Fischer has shown that the cilia of Bacteria possess a similar power of independent locomotion, while Hofmeister, Pfeffer, Hauptfleisch, and Gerasimoff have all found that streaming may continue in non-nucleated fragments of cells of both Phanerogams and Cryptogams[2].

In all the experiments carried out upon protoplasts covered by a cell-wall, the possibility of the existence of fine plasmatic connexions between the nucleated and non-nucleated portions of the cell has been overlooked. That this is by no means a negligible possibility is shown by the fact that Palla[3] concluded, in opposition to the previously accepted view[4], that a renewed formation of the cell-wall was possible around both nucleated and non-nucleated fragments of protoplasm. Townsend[5] has, however, since shown that Palla overlooked the existence of fine plasmatic threads connecting the nucleated and non-nucleated fragments, and that in the absence of these threads no power of forming a new wall is possessed by the latter. Hence it seemed quite possible that the same explanation might apply to the continuance of streaming movements in non-nucleated fragments in Phanerogamic cells.

There are several methods of obtaining completely isolated non-nucleated cytoplasms, and if these remain uncovered by a cell-wall, we have a double security against error. Cells containing protoplasts fragmented by plasmolysis or by induction shocks may be opened and the contents allowed to escape in an isosmotic solution of sugar. Streaming may often not recommence, but in many cases it may be shown by non-nucleated fragments for a few hours or even days afterwards (*Vallisneria, Elodea, Tradescantia, Trianea*). In intact cells the protoplasmic connexions may be broken or destroyed by the localized application of strong induction currents[6]. If the thread is not as yet covered by cellulose, it breaks and is retracted, but streaming may continue apparently unaffected in successful experiments, although it always ceases sooner in non-nucleated fragments than in nucleated ones. Pollen-tubes (*Narcissus, Lilium*) often exhibit a natural process of fragmentation when grown on gelatine or in certain fluid media, and streaming movements may occa-

[1] Hertwig, Zelle, 1893, p. 264; Verworn, Allgem. Physiologie, 1895.

[2] Fischer, Bacteria (Clar. Press), 1900; Hofmeister, l. c., p. 52; Pfeffer, Zur Kenntniss d. Plasmahaut u. d. Vacuolen, 1890, p. 279; Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV, p. 172; Gerasimoff, Ueber die kernlosen Zellen bei einigen Conjugaten, 1892, 1896.

[3] Flora, 1890, p. 314.

[4] Klebs, Bot. Unters. a. d. Bot. Inst. zu Tübingen, 1888, Bd. II, p. 552.

[5] Jahrb. f. wiss. Bot., 1897, Vol. XXX, p. 484.

[6] Townsend, l. c., p. 484.

sionally be seen in non-nucleated fragments which have no protoplasmic connexions with the nucleus, or which may even be cut off from it by ingrowths of cellulose [1].

Another mode of experimentation is to replace fragmented cells with plasmolyzed protoplasts in more dilute solutions, or ultimately water, after the nucleated portions have become covered with a new cell-wall. The expansion is naturally more marked in the non-nucleated portion than in that covered by a cell-wall, even when the latter is still thin. The rapidity of streaming usually increases, but it ceases more rapidly in the non-nucleated portion than normally. As the percentage of water in the protoplasm increases, its respiratory activity will increase, while its viscosity decreases. Hence the increased velocity. When the restraining influence of the nucleus is removed, either katabolism seems to preponderate over anabolism, or assimilation decreases, so that the non-nucleated cytoplasm wastes away even under optimal nutritive conditions. Hence, in water or dilute sugar solution the increased respiration causes a more rapid consumption of the available plastic material, so that although the velocity of streaming is temporarily enhanced, the duration of the movement is lessened.

SECTION 24. **Changes of Concentration and of Turgidity.**

The effect of these has already been discussed from a purely physical point of view, but in addition a physiological stimulating action may be exercised. Thus the shock of immersal in dilute saline solutions suffices to cause a temporary stoppage of streaming lasting from one to ten minutes, which is very different in its origin from the gradual slowing and ultimate cessation of streaming which may be produced by the chemical action of the dissolved substance. These facts were first observed by Dutrochet in *Chara*, and Hörmann finds that a similar shock-stoppage may readily be produced in *Nitella* [2]. A shock-stoppage may also be produced in *Elodea*, *Vallisneria*, and *Trianea* by suddenly applying nearly isosmotic saline solutions, but this result is naturally more difficult to attain in cuticularized hair-cells (*Tradescantia*, *Urtica*, *Cucurbita*). After the cells have accustomed themselves to the concentrated solution, a shock-stoppage may again be produced by suddenly immersing them in water (cf. Dutrochet, l. c.).

Hörmann found that if one half of a cell of *Nitella* was immersed in water, and the other in 5 per cent. sugar solution, streaming soon recommenced in both halves, but was slower in the end in sugar solution than in that in water. He regards this as the result of the tonic stimulating action

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[1] Cf. Ewart, Trans. Liverpool Biol. Soc., 1895, Vol. IX, p. 199.

[2] Dutrochet, Ann. sci. nat., 1838, p. 71; Hörmann, Studien über Protoplasmaströmung der Characeen, Jena, 1898, p. 51.

of the sugar solution. The author is able to corroborate this observation, although the difference of velocity is not always perceptible, especially in short cells, while in long ones the slowing or quickening of streaming is exhibited shortly after crossing the boundary line between the two fluids. It can in such cases sometimes be clearly seen that the streaming layer is thicker in the part immersed in sugar solution than in that in water, and this although the sugar solution by withdrawing water from the protoplasm would tend to diminish its volume. The explanation of the difference of velocity is a very simple one, namely, the sugar solution withdraws water from the protoplasm, increases its viscosity, and hence decreases the velocity of streaming. As the stream enters the other half of the cell this water returns, and the normal velocity is regained shortly after the cell has crossed the boundary line. The net result is, therefore, an increase in the time of a complete rotation. If the action were a stimulating one, as Hörmann supposes it to be, we should have an instance of a localized stimulus which, acting upon an irritable and physiologically conducting substance, either produces a localized effect without any transmission to neighbouring equally irritable and physiologically connected parts, or which is propagated to a very slight extent only in the direction of streaming. This is, however, a physiological impossibility, since the stimulus when first applied causes an almost simultaneous temporary stoppage over the entire cell.

The greatest difference of velocity observed amounted to one half of the rate of the part in water, but was usually less pronounced. Now the removal of not more than 17 to 18 per cent. of water from ordinary egg-albumin nearly quadruples its viscosity, and since, other things being equal, the velocity is inversely proportional to the viscosity, the observed difference of velocity is just such as might be produced by the localized change in the percentage of water, and its attendant alteration in viscosity, aided possibly to a slight extent by localized alterations in the respiratory activity.

This action is, therefore, a direct physical one, although after a time a stimulatory influence becomes perceptible in the form of temporary stoppages of streaming in the part immersed in water. These might be regarded as an attempt on the part of the cell to maintain the same average velocity in the two halves, but frequently the stoppage extends over the entire cell, owing either to a temporary derangement of the motor-mechanism, or to disturbances in the metabolism on which the latter is dependent, produced as the result of the continued exit and entry of water. That these stoppages are not shock-stoppages, rendered possible by an increase in the excitability of the cell after prolonged immersion, is shown by the fact that the excitability to other stimuli is diminished by such treatment, and that ultimately the cells are killed. The sugar solution

probably acts as a physical stimulus and not as a chemical one, such as is exercised by many dilute solutions, for when cells are completely immersed in 1 to 3 per cent. cane-sugar solution, a nearly constant retarding action seems to be exercised.

SECTION 25. The Influence of Temperature.

In 1774 Corti stated that streaming returned to cells of *Chara* which had been frozen at −5° C. and then thawed, but Dutrochet [1] found that the minimum temperature for streaming in *Chara* was −1° C., and, as a matter of fact, vegetating cells of *Chara* are killed by freezing at −5° C. Dutrochet also found that in cells of *Chara* placed in water at 34° to 40° C. streaming at first slowed, but subsequently became more rapid, whereas at 45° C. it soon permanently ceased. The first slowing is, however, merely a shock effect, and if the rise of temperature is not too rapid, a continuous increase is shown up to, or even above, the permanent optimum temperature. The cardinal points obtained by different investigators are given beneath.

Author [2].	Plant.	Minimum.	Optimum.	Maximum.
Dutrochet	*Chara fragilis*	0° C. to 1° C.		45° C.
Sachs	*Cucurbita pepo*	10° to 11°		
	Solanum lycopersicum	12°	30° C. to 40° C.	40° to 50°
	Tradescantia	12°		
Cohn	*Nitella syncarpa*	2°		
Velten	*Vallisneria spiralis*	0° to 1°	38·7°	45°
	Elodea canadensis	0°	36·2°	38·7°
	Chara foetida	0°	38·1°	42·8°

Sachs states (l. c., p. 39) that heat-rigor and cold-rigor may sometimes be prolonged for hours without permanent injury, and has also shown that the resistance to extremes of temperature is greater when in air than when immersed in water.

Velten [3] found that the increases in velocity become greater and greater for each degree as the temperature rises from the minimum to the optimum, and states that at each temperature a corresponding velocity is immediately assumed, which undergoes no subsequent change. This latter statement is entirely misleading, but the former one is supported by Schaefer's calculation from Nägeli's results that the direct response to rises of temperature increases very nearly in geometric proportion to rises of temperature between 10° C. and 30° C.[4] According to Hauptfleisch, rapid rises or falls of temperature may induce streaming wherever a tendency to

[1] Ann. sci. nat., 1838, p. 25.

[2] Dutrochet, l. c., pp. 25–7; Mémoires, 1837, I, p. 561; Sachs, Flora, 1863–4, p. 39; Cohn, Bot. Zeitg., 1871, p. 723; Velten, Flora, 1876.

[3] Flora, 1876, pp. 210, 214.

[4] Schaefer, Reaktion des Protoplasmas auf thermische Reize, Flora, 1898, Vol. LXXV, p. 135.

this form of activity exists, although slow changes produce no such result. The same author[1] states that the minimum temperature for streaming is 0° C., the optimum 37° C. to 38° C., and the maximum 41° C. to 42° C., although the leaf of *Elodea* may show active streaming at 43° C. and slow streaming at 52° C.

Attempts to determine the cardinal points of single plants to a degree or a fraction of a degree are largely futile, since not only do the cardinal points vary according to the plant or cell examined, but they also depend upon (1) the age and condition during experimentation, (2) the external medium, (3) the duration of the exposure, (4) the supply of oxygen, (5) the rapidity with which the temperature alters.

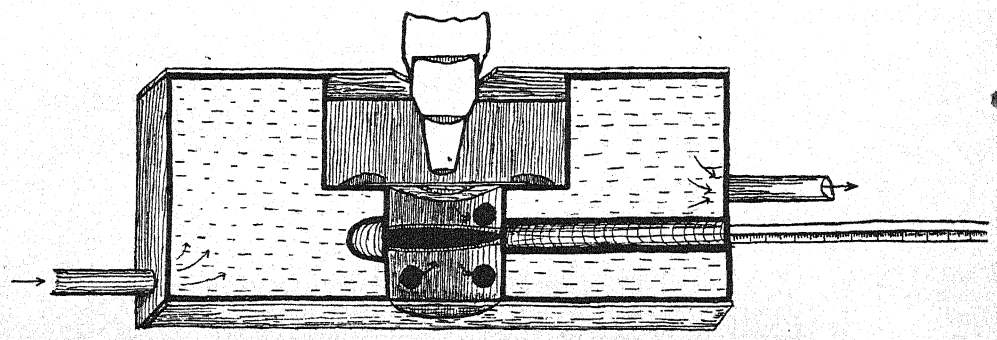

FIG. 9. Combined hot stage and gas chamber.

Streaming may permanently cease in cells suddenly raised to a temperature at which it continues for a longer or shorter time, if the rise is more gradual. Hence a cell may be killed by immersal in hot water, though not if plunged into air at the same temperature. Similarly, a cell which is kept moist can withstand a slightly higher temperature in dry air than in air saturated with water-vapour, owing to the cooling effect of evaporation. Again, at high temperatures the cell consumes more oxygen, and, owing to the decrease in the solubility of this gas as the temperature rises, it is absorbed in sufficient quantity with greater difficulty from hot water than it is from cold water or hot air. The same applies even to green cells exposed to light, for at high temperatures the power of photosynthesis is suppressed. Hence in all test experiments the preparations were placed in thin films of water enclosed in a hot chamber[2] filled with air kept saturated with moisture. A slight interval for adjustment was allowed between each change of temperature, and in order to avoid any

[1] Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Bd. XXIV.

[2] The hot stage devised by the Cambridge Scientific Instrument Company was at first used, but the above modification of it (Fig. 9) yields more accurate results, since the loss of heat by radiation through the cover-glass is almost entirely avoided.

shock-effect, the changes were made at the rate of from 1 to 10° C. per minute. At the end of each experiment the velocity of streaming was noted at room-temperature, in order to determine whether any internal change had been produced. Whenever this occurs the results are of course useless for comparison. Prolonged exposure to a moderately high temperature ultimately exercises a depressant influence on streaming in spite of its primary direct acceleration. This may be somewhat analogous to the effect of a high temperature in inducing lassitude in warm-blooded animals. Thus, after being at 37° C. to 38° C. for three days, *Chara fragilis* shows slow streaming, becoming active in a few minutes at 20° C., while *Elodea* shows none, although fairly active streaming appears after five to fifteen minutes at 20° C. A day's exposure to a temperature of 40° C. to 45° C. suffices to cause a permanent stoppage of streaming and ultimately death in *Chara*, *Nitella*, *Elodea*, *Spirogyra*, *Sagittaria*, *Tradescantia*, *Lepidium*, pollen-tubes, and root-hairs.

Similarly, prolonged exposure to low temperatures may cause a complete or nearly complete stoppage of streaming. Thus, after six hours at 0° C. to 0·2° C., only very slow streaming is shown by *Chara*, *Nitella*, and *Elodea*, while after two days only the larger axial cells of *Nitella* exhibit very slow streaming, the latter becoming active or nearly active in all or nearly all the living cells after a quarter of an hour at 20° C. In the first two plants a stoppage of streaming indicates that the limit of resistance is nearly reached or even surpassed. A change of temperature may directly affect the rate of streaming by changing (1) the viscosity of the protoplasm, (2) the energy consumed in streaming. Only a fraction of the energy of respiration is ever used in streaming, and since every protoplast is capable of regulating and proportioning its own activity, it does not necessarily follow that an increased respiration involves a proportionate increase in the energy of streaming. As the temperature rises, however, the viscosity decreases less and less for each degree, whereas the increments of velocity progressively increase between 10° C. and 30° C. It follows, therefore, that the increased activity of streaming is mainly due to the diversion of an increased fraction of the respiratory energy into this channel. Above 30° C., however, the successive increments of velocity for each rise of temperature progressively decrease, and the influence of the changes of viscosity becomes more prominent. The almost immediate stoppage occurring at temperatures above 55° C. to 60° C. is the result of partial coagulation, but the more gradually produced cessation taking place at 45° C. to 55° C. is probably the result of a functional derangement of the motor-mechanism.

In all cases it must be remembered that the regulatory mechanism may come into play so that the *tempo* at first assumed may not be the same as that exhibited after longer exposure.

The following detailed examples will illustrate these points:—

Nitella translucens	Temperature	25° C.	30° C.	30° C.	40° C.	40° C.	40° C.	40° C.	45° C.	45° C.	45° C.	45° C.
	Duration of exposure	24 hrs.	5 min.	+ ¼ hr.	5 min.	+ ¼ hr.	+ ¼ hr.	+ ¼ hr.	1 min.	+ 5 min.	+ 15 min.	+ 20 min.
	Rate in secs. per 2 mm.	35	25	26	19–20	26	31	39	37	40	58	72
Infusoria	... ...	...	...	fully active	active	less active	sluggish	...	...	dead and burst		no movement
Bacteria	... ...	...	...				few moving	...	...	all at rest	...	
Vorticellae	... ...	...	...				occasional contractions	...	...	occasional contractions	Cilia nearly at rest	
Rotifers	... ...	...	...					...	...	feeble twitching	...	movement ceased

On lowering the temperature to 20° C. streaming slows and ultimately ceases, whereas the Rotifers and a few Vorticellae recover and again move actively. If the temperature is raised 5° C. every two or three minutes, streaming may not entirely cease until from 55° C. to 60° C. is reached, whereas if suddenly plunged into water at from 40° C. to 50° C. it immediately and usually permanently ceases, and the same ultimately occurs after prolonged exposure to 40° C. to 50° C. There is, therefore, a particular rate of rise of temperature at which streaming persists longest. A very sudden rise does not give any time for accommodation, and completely deranges the motor-mechanism at relatively low temperatures. A very slow rise extending over hours or days exercises a cumulative effect, and hence again lowers the maximal temperature.

After an exposure of ten minutes to 50° C. irregular streaming may still be present in *Nitella*, and may become normal again at 20° C. Similarly, if the moment streaming has ceased at 69° C. the preparations are cooled, in a few cases the cells remain living, though streaming is frequently slower than at first. Cells killed by sudden heat-rigor do not contract, or only slightly after several hours. This is obviously due to the rapid coagulation of the protoplasm, and the fluctuations in rapidity often shown at high

temperatures may partly be due to partial coagulation, and partly to passing disturbances in the motor-mechanism.

Chara foetida	Temperature	20° C.	30° C.	40° C.	40° C.	40° C.	40° C.	50° C.	50° C.	50° C.
	Duration of exposure	24 hrs.	5 min.	5 min.	+ ¼ hr.	+ ½ hr.	+ 1½ hr.	1 min.	5 min.	+ 10 min.
	Seconds in crossing 2 min.	40	28	20	20	30	50	45	125	slow creeping.

If raised only from 40° C. to 45° C. a similar transient acceleration followed by a progressive retardation may be shown, without the power of recovery being necessarily lost. When now rapidly cooled to 20° C. a further retardation may ensue, followed usually after a few minutes to an hour or so by a steady increase of velocity up to approximately the previous initial velocity. If, however, the temperature falls rapidly to from 35° C. to 38° C., and then very slowly to 20° C., the curious anomaly may be seen that a falling temperature is accompanied by an increasing velocity.

The age of the cell is a potent factor in determining the optimal and maximal temperatures for streaming, these being much lower in young cells than in adult ones. Moreover, streaming is more easily stopped in young cells without inflicting permanent injury. Thus in young cells of *Nitella* and *Chara*, in which streaming has just commenced, the latter became slow at 40° C. and ceased at 45° C., when raised not too rapidly to these temperatures. At 20° C. it recommenced in from a quarter of an hour to several hours afterwards. In the case of a slightly older cell, the velocity of streaming began to decrease at 40° C., was slow at 45° C., and ceased at 48° C. to 50° C., recovery occurring if the exposure had not been unduly prolonged. Finally, in adult medullary or internodal cells streaming was usually very slow at 50° C., almost ceased at 60° C., and completely at 65° C., no recovery occurring if the cell was longer than five minutes above 60° C. Indeed, five minutes' exposure to 60° C. suffices usually to affect the cell fatally, without streaming entirely ceasing during the actual exposure.

At each temperature a velocity of streaming is assumed which may or may not alter on prolonged exposure. Above 30° C. the immediate velocity is, in the absence of a retarding shock-effect, always greater than that exhibited a few hours or a few minutes afterwards. The first effect is to decrease the viscosity of the moving layers and to increase the energy of respiration, but before long the regulatory mechanism comes into play, and either less energy is employed in this manner than before or it is employed less effectively. The viscosity of the protoplasm may also be increased by

a withdrawal of water from it, or by chemical or physical changes in its substance. The net result is a decrease in the velocity of streaming. At temperatures above 40° C. a continuous retardation is shown, leading ultimately to a complete cessation accompanied by an irremediable overthrow of the vital equilibrium. Death is here the result of heat pyrexia. The almost immediate stoppage at very high temperatures is the result of the partial or complete coagulation of the protoplasm.

At temperatures lying between 10° C. and 30° C. the immediate streaming *tempo* is usually also the permanent one, provided no other factors come into play, such as an inadequate supply of oxygen, or an insufficiency of food. Under either of these latter circumstances a rise of temperature brings about a retardation or cessation of streaming sooner than would otherwise have been the case.

Below 10° C. the acceleration due to a rise of temperature is usually not as great as it subsequently becomes. This is probably because the semi-dormant vital activity is not immediately awakened to the full extent possible at the particular temperature, and the same thing commonly occurs as regards growth, photosynthesis, &c., when plants that have been kept at a low temperature for some time are brought into a warm room.

In the case of plants in which streaming is usually secondary in character (*Elodea, Vallisneria*), and less intimately connected with the vitality of the cell than it is in *Chara* and *Nitella*, there is a greater tendency to internal changes which modify the natural response to a change of temperature. Thus, if leaves of *Elodea* are suddenly raised from 18° C. to 35° C., streaming commences in one to two minutes, and becomes active in half to one hour. A similar sudden rise to 40° C. produces a more rapid response, although after two to three hours at 40° C. streaming is slower than at 35° C. If now raised to 50° C. the velocity increases slightly in the first one or two minutes, but in fifteen minutes is from $\frac{1}{4}$ to $\frac{1}{5}$ the velocity at 40° C. If now allowed to fall slowly to 30° C. the velocity steadily increases until greater than at any previous temperature. The character of the material, therefore, changed during experimentation. Similarly, in cells of *Vallisneria* showing slow streaming the latter may steadily decrease from 35° C. onwards, ceasing after one minute at 50° C., although on lowering to 30° C. it soon becomes rapid.

Hence adult cells exhibiting active and well-established streaming should be used for experimentation. Leaves of *Elodea* may be treated with dilute glycerine, and then washed in water, while section-cutting usually affords a sufficiently powerful stimulus to prolonged streaming in *Vallisneria*.

Vallisneria spiralis.

Temperature	20° C.	30° C.	30° C.	30° C.	40° C.	40° C.	45° C.	45° C.	50° C.	50° C.	55° C.	40° C.	35° C.	25° C.	20° C.	20° C.
Duration	24 hrs.	1 min.	+ 2 min.	+ 15 min.	1 min.	+ 15 min.	1 min.	+ 15 min.	1 min.	+ 10 min.	1 min.	3 min.	10 min.	20 min.	30 min.	2 hrs.
Rate per ½ mm. in secs.	50	33	30	34	20	24	25	28	35	slow creeping or irregular	ceased	irregular twitching	slow creeping	still slow	65	55

Elodea canadensis.

Temperature	25° C.	30° C.	40° C.	40° C.	40° C.	45° C.	50° C.	45° C.	50° C.	50° C.	25° C.	55° C.	55° C.	55° C.	25° C.	20° C.
Duration	24 hrs.	5 min.	5 min.	+ ¼ hr.	+ ½ hr.	5 min.	5 min.	+ ¼ hr.	+ 10 min.	+ ¼ hr.	+ ¾ hr.	1 min.	+ 5 min.	+ 10 min.	+ 15 min.	½ hr.	24 hrs.
Time of one rotation in secs.	24	21	14	15	17	15	18	16	22	34	26	16	21	28	42	29	28

If the temperature is more rapidly raised, the velocity of streaming goes on increasing up to over 45° C., becomes irregular and jerky at 55° C., and ceases entirely after five minutes at 60° C., but even then the power of recovery is frequently retained.

Whenever streaming is stopped by high temperatures, the chloroplastids tend to ball together more or less completely, slowly spreading out again when streaming is resumed. Irregular twitching movements first occur, and in some cases the chloroplastids appear to be jerked forwards and then slightly backwards with an elastic recoil, just as if the protoplasm had undergone partial coagulation and contained highly viscous threads of myosin-like proteids.

Similar results were given by *Elodea canadensis*.

If actively streaming cells are raised 4° C. per minute from 20° C. upwards, streaming is slower at 40° C. than at 20° C. (18 : 34), but only ceases when 60° C. is reached and the cells are fatally affected. If

suddenly raised to 60° C. streaming ceases within two minutes, and if immediately returned to 25° C. does not recommence until after fifteen minutes to five hours. The direction of streaming is occasionally reversed in cells bordering on ones which have been killed by the exposure[1].

SECTION 26. Effect of Sudden Changes of Temperature.

According to both Dutrochet (l. c.) and Hofmeister[2], a sudden and pronounced change of temperature may act as a stimulus temporarily inhibiting or retarding streaming in *Chara* and *Nitella*. Velten[3] expressly denies this, but Hörmann[4] was able in part to confirm the older observations. According to this author, a marked and sudden fall of temperature always causes a temporary stoppage, although a sudden rise of temperature, if below 45° C., always produces an acceleration, whereas above 45° C. retardation may ensue. Localized cold applied to one end of a warm cell of *Nitella* causes an almost immediate stoppage of streaming, and similarly, if a cell at 5° C. has one end suddenly warmed to 30° C., streaming also ceases after a latent period of ten to thirty seconds. In this latter case the stoppage is also due to a *fall* of temperature and occurs when the protoplasm warmed at one end is cooled by streaming into the cold part of the cell, the long latent period representing mainly the time of streaming past the warm end.

The above action is that of a shock-stimulus producing a temporary disturbance of the motor-mechanism. When different regions of a cell are kept at different temperatures, streaming is slower, and the stream thicker, over the cold region than over the warm one. Thus, with one half at 4° C. and the other at 16° C., streaming may be more than twice as rapid in the second half than in the first. The relative viscosities of albumin at these temperatures are as 10 : 7, so that a large part of the difference of velocity is probably due to the different viscosities of the streaming plasma in the warm and cold halves of the cell. A difference of temperature of 25° C. to 35° C. (2° C. at one end, 37° C. at the other) soon causes pronounced aggregation and death in two to three hours. Hörmann denies that a sudden rise of temperature ever causes a stoppage unless the maximal point is reached or passed. Klemm[5] has, however, shown that when hairs of *Momordica* are suddenly raised from 18° C. to 45° C. streaming ceases momentarily, is then resumed again, and ultimately ceases. The same is the case when cells of *Nitella* and *Chara* are suddenly raised from

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[1] Streaming takes place normally in opposite directions on the two sides of each dividing wall.
[2] Die Lehre von der Pflanzenzelle, 1867, p. 53.
[3] *Flora*, 1876, p. 214.
[4] Protoplasmaströmung bei den Characeen, Jena, 1898, p. 44.
[5] Jahrb. f. wiss. Bot., Bd. XXVIII, p. 15; cf. also Sachs, Flora, 1864, p. 65.

10 or 15° C. to 45° C. The intensity of the stimulus is proportional to the rapidity of the change, and hence a rise of 25 or 30° C. suffices to produce a temporary stoppage of streaming without any injurious after-effect in the above plants, and also in *Elodea*, *Vallisneria*, and *Tradescantia* if cells are suddenly transferred from cold (10° C.) to hot (35° C. to 40° C.) water.

A similar shock-effect is produced when a streaming cell is suddenly subjected to a low temperature. Thus Kühne[1] found that when hairs of *Tradescantia* were cooled to −14° C. in five minutes, streaming ceased and the protoplasm separated into globules, but became normal again within ten minutes at room-temperature. Similar results were obtained by Hofmeister with an exposure of ten minutes to −8° C., and by Klemm[2] on subjecting cells of *Chara* and hairs of *Momordica* and *Trianea* to temperatures of −5° C. to −6° C. for ten minutes. In the older experiments the registered temperature was probably lower than that to which the plants were actually exposed, but even Klemm's observations form no sure proof of a shock-effect, for the temperatures given are below the minimal points for prolonged streaming in these plants, and they are all killed by being frozen at these temperatures[3]. Satisfactory proof was, however, easily obtained in the following manner:—Cells of *Chara*, *Nitella*, &c., were enclosed in fine capillary glass tubes partly filled with water, which were plunged into a freezing-mixture of snow and salt for from twenty seconds to two minutes. The tubes were immediately placed on the microscope stage and examined, when it could often be seen that streaming is at first present, but then suddenly temporarily ceases, as the result of the after-effect of the shock of cooling. Rapid examination is required, since the latent period of stimulation is rarely as much as ten seconds. Hence a better mode of experimentation is to place the capillary tube within a large flattened one which rests on the microscope stage, and through which cooled brine can be passed[4].

Staminal hairs of *Tradescantia*, root-hairs of *Trianea*, and leaf-cells of *Chara* and *Nitella*, if lowered from 10° C. to 2° C. in five to ten minutes, still show slow streaming, which is progressively retarded and ceases in one to a few hours. If the preparations are brought to 15° C. immediately on cessation, streaming is actively resumed after twenty minutes. Longer exposure, if not fatal, prolongs the latent period of recovery slightly. The immediate decrease of velocity is largely due to the increased viscosity of the protoplasm at low temperatures, but the subsequent steady fall is

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[1] Unters. über das Protoplasma, 1864, p. 101.

[2] Hofmeister, Zelle, p. 54; Klemm, l. c., p. 16.

[3] Cf. Ewart, Ann. of Bot., Vol. XII, 1898, pp. 365–6.

[4] The rapid condensation of water upon the cold tube is apt to be troublesome, but it can almost entirely be avoided by directing a jet of dried air upon the outside of the tube just beneath the objective.

probably the result of the cumulative depressant influence of the low temperature upon the vital activity of the cell as a whole.

A similar stoppage of streaming is produced by prolonged exposure to temperatures lying just above the freezing point (0° C. to 1° C.), six to ten hours usually sufficing in the case of *Trianea*, *Tradescantia*, and *Vallisneria*, but periods of one to two days being required by *Chara* and *Elodea*, and three to four days by large axial cells of *Nitella*.

SECTION 27. Influence of Temperature during Anaerobic (Intramolecular) Respiration.

The hot chamber used for these experiments was provided with exit- and entry-tubes for gases, and the cover-slip after its rim had been smeared with vaseline was sealed with wax, melted shellac, or plaster of paris and shellac, according to the temperature. The same precautions as previously mentioned were used to obtain perfectly pure oxygenless hydrogen.

When green cells are examined, their power of photosynthesis may be temporarily inhibited by etherization. Streaming is, however, also affected, weak doses accelerating and stronger doses retarding it. Doses sufficient to cause a slight retardation of streaming in *Elodea* usually inhibit the power of CO_2-assimilation, so that streaming ceases in hydrogen in about the same time whether the preparations are kept in darkness or exposed to light.

Removal of the ether vapour by a fresh current of hydrogen may shortly be followed by a resumption of CO_2-assimilation and a recommencement of streaming, if the exposure has been short. With more prolonged exposures, recovery may not take place in hydrogen although it may in air, while with still longer exposures the power of recovery is entirely lost. Unfortunately streaming soon ceases in *Elodea* in the absence of free oxygen, while *Chara* and *Nitella* are soon fatally affected by doses of ether sufficient to produce the required effect.

Above 38° C., however, *Chara* and *Nitella* cease to evolve oxygen, and hence above 40° C. the power of CO_2-assimilation must be entirely or almost entirely in abeyance, so that at high temperatures chlorophyllous cells yield in light approximately similar results to those given by the colourless rhizoids.

In general it may be said that between 5° C. and 45° C. the influence of a rise or fall of temperature upon the velocity of streaming is both absolutely and relatively less pronounced than when aerobic respiration is fully active, the cells behaving as if in a semi-dormant condition. This is probably because the temperature affects the katabolism and hence the liberation of energy to a relatively less degree than in the presence of oxygen.

With regard to the optimal and maximal points, their determination is somewhat difficult, for successive observations frequently fail, either owing to the non-recovery of the cell or a permanent alteration of its *tempo*. By frequent repetitions, however, the interesting fact was established that with short periods of exposure the maximum point for streaming is raised during anaerobic respiration from 3° C. to 5° C., and the optimum by from about 5° C. to 8° C., these two cardinal points hence being nearer together than is normally the case.

In the absence of one stimulus (oxygen) the other (temperature) must apparently be intensified to produce the maximal velocity.

With prolonged exposures, however, the maximal point is lowered by as much as 5° C. or 10° C. below the normal, whereas even after two or three hours in pure hydrogen the optimum point either approximates closely to that for aerobic respiration or may still be slightly above it. In such cases a rise of only a few degrees above the optimum temperature may cause the velocity of streaming to fall abruptly to nil. In all cases the recovery from the effects of exposure to high temperatures is much retarded and often permanently so, in an atmosphere of hydrogen, especially if no internal supply of oxygen by CO_2-assimilation is possible. From the above facts it may safely be concluded that the stoppage produced by prolonged exposure to temperatures approaching 45° C. in the presence of oxygen is not due to a partial coagulation of the protoplasm, but mainly to some disturbance in the motor-mechanism. A partial coagulation and consequent increase of viscosity may take part in the retardation and ultimate stoppage produced between 45° C. to 55° C., and above 55° C. is probably mainly responsible for the stoppage. Complete coagulation involving irremediable injury usually takes place subsequently to the stoppage, whereas as a general rule recovery is possible from a stoppage caused by slight partial coagulation, or by a temporary disturbance of the motor-mechanism.

When the temperature is lowered, streaming ceases sooner in the absence of oxygen than in its presence, i.e. the minimal point is raised 2 to 5° C. during anaerobic respiration. This is probably the result of the decreased liberation of energy acting conjointly with the increased viscosity at low temperatures.

SECTION 28. **The Influence of Light.**

A slight retardation of streaming in the sensitive plasmodia of Myxomycetes was noticed by Hofmeister and by Baranetzsky[1] when they

[1] Hofmeister, Pflanzenzelle, 1867, p. 21; Baranetzsky, Mém. de la Soc. des sci. nat. de Cherbourg, 1876, XIX.

were exposed to light. According to Borscow and Luerssen[1] this action of light is a general phenomenon, the red rays exercising the greatest effect and causing a retardation and ultimate cessation of streaming. This result is, however, owing to the heating effect of the red rays, and if the preparations are kept cool, it is easy to see that the blue rays are most effective (in the presence of oxygen). On the other hand, other authors[2] could detect no influence of light on streaming. This was probably owing to the use of light of feeble intensity, for Pringsheim[3] has shown that exposure to intense light causes a pronounced retardation and rapid cessation of streaming in *Nitella*, *Tradescantia*, and *Spirogyra*, while the author has extended these observations to *Chara*, *Elodea*, *Vallisneria*, as well as to *Hydra viridis* and *Vorticella campanula*[4].

The intensity of the illumination necessary is usually very much over-estimated. For example, sunlight passed through cold alum solution, and concentrated by a lens to a photochemical intensity of about eight times that of bright direct sunlight, causes a cessation of streaming in *Elodea* leaves within six minutes, while if the alum solution is removed, a complete temporary or permanent stoppage is produced in from one to four minutes. Sections of leaves of *Vallisneria* are even more sensitive, but *Chara* is usually less so. Thus five minutes' exposure may produce complete rigor on the margins of leaves of *Elodea*, whereas eight minutes' similar exposure may be required to produce the same effect on end-cells of *Chara*. In the latter case it can usually be seen that after the first twenty or thirty seconds streaming is accelerated, sometimes to twice the original speed, then slowing rapidly after three to five minutes, and ceasing or becoming very slow by the time the chloroplastids are bleached. When slow streaming is still present at the end of a period of exposure, it may go on slowing until it permanently ceases, or may gradually acquire its original velocity. The first acceleration is probably due to the heating effect, which can never be entirely eliminated, and it is always more marked if the preparation is in a cool medium to commence with. If the preparation is previously warmed no acceleration can usually be detected, but this observation is of little value, for whenever streaming is at, or nearly at, its maximal velocity, a new stimulus must either exercise no appreciable effect or must cause a retardation.

Six to eight hours' continuous exposure to bright direct sunlight suffices to make streaming cease or become very slow in *Chara* and *Elodea*, while under weak illumination it is usually fairly active again in a quarter of

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[1] Borscow, Bull. d. l'acad. de St.-Pétersbourg, 1868, XII; Luerssen, Einfluss des rothen und blauen Lichtes auf die Strömung des Protoplasmas, 1868.

[2] Cf. Hauptfleisch, Jahrb. f. wiss. Bot., 1892, Vol. XXIV, p. 173.

[3] Jahrb. f. wiss. Bot., 1882, Bd. XII, pp. 326–44.

[4] Ewart, Ann. of Bot., 1898, Vol. XII, pp. 383–90.

an hour to two hours, even in a few cases in which it ultimately permanently ceases.

Momentary exposure to darkness or bright light seems to have no influence on streaming, but if preparations kept in darkness for some time are suddenly exposed to concentrated sunlight, a temporary stoppage lasting for a few seconds to a minute, or in *Chara* and *Nitella* a local retardation, may often be seen. The latter is followed by a slight acceleration, after which the streaming rapidly decreases and ultimately ceases if the exposure is continued.

If plants of *Chara* or *Nitella* are kept some days or weeks in darkness, streaming becomes very slow, or moderately slow if the water is well aerated. On exposure to bright diffuse light, streaming quickens within five minutes, and may be four or five times as rapid within a quarter to half an hour. Moore [1] concluded from similar observations on *Chara vulgaris* that light acted as a direct stimulus accelerating streaming. If, however, the plants are previously well aerated, streaming is more rapid to commence with, and the acceleration is lessened and delayed by five or ten minutes. If in addition the light is rendered as athermal as possible, a longer exposure is necessary to produce any perceptible effect, and the ultimate acceleration is still less pronounced. Obviously, therefore, the acceleration is partly due to (1) a heating effect and (2) an increased percentage of oxygen within the cell, for the chloroplastids of *Chara* can immediately resume the assimilation of carbon dioxide even after the prolonged absence of light.

When the above precautions are taken, a noticeable acceleration on exposure to light only occurs in specimens which have been in darkness for two or three weeks, and are partially starved. In this case exposure to light produces a renewed supply of food, and hence also of energy for streaming.

SECTION 29. **Other Forms of Radiant Energy.**

Although streaming cells are very sensitive to electrical currents, they seem to be insensible to electrical waves propagated through the ether. At any rate streaming cells placed in various positions between two syntonic Leyden jars, one of which was rapidly charged and discharged, were unaffected, however well the second jar responded. It is, however, possible that by a better arrangement positive results might be obtained.

Atkinson [2] concluded that the Röntgen rays exercised no perceptible influence on plants, but this was probably owing either to the exposure

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[1] Journ. Linn. Soc., 1888, Vol. XXIV, p. 246.

[2] Atkinson, Science Progress, 1898, Vol. VII, pp. 7–13; Lopriore, Nuova Rassegna, Catania, 1897; cf. also Bot. Centralbl., 1898, Bd. LXXIII, p. 451.

being too short, or too weak in character, for Lopriore has shown that the Röntgen rays at first accelerate streaming in *Vallisneria*, but that if the action is prolonged streaming is retarded and the cells injuriously affected. The influence of the absence of light or of temporary weak illumination is so slight as to be negligible, and hence these results are due to the direct action of the Röntgen rays, and prolonged exposure to them seems to produce a distinct effect upon animal organisms also.

With regard to the influence of the prolonged absence of light, Dutrochet [1] found that streaming ceased in *Chara* after twenty-four to twenty-eight days' darkness, but this was merely the result of starvation, for the author has shown that if the darkened parts remain attached to the parent plant, the cells may remain living and showing streaming for five to eight weeks [2]. Light as such does not therefore form a directly essential factor in the maintenance of streaming movements.

SECTION 30. **Mechanical Stimuli.**

That a retardation or temporary cessation of streaming may be caused in *Chara* and *Nitella* by mechanical shocks has long been known [3], although Pfeffer has shown that mechanical vibrations exercise no effect upon streaming in hair-cells of *Hyoscyamus* and *Datura*, while Hörmann found that mere contact or gentle rubbing with a soft brush produced no effect on streaming in *Nitella syncarpa* [4]. Similarly regular (siren, organ-pipe, violin) or irregular (explosions) vibrations of the air produce no perceptible effect upon streaming in cells of *Chara* and *Nitella* upon which they freely impinge. The inertia of the cell-wall and its fluid contents is, however, very great as compared with that of the air, and hence it is still possible that very violent vibrations of considerable amplitude might produce some perceptible effect.

Hörmann states that rapid changes of pressure in the surrounding medium (water) exercise no influence upon streaming in *Nitella syncarpa*. His experiments were carried out by placing the cells in water in a flat glass tube connected with a manometer tube filled with mercury. By raising or lowering this tube, pressures up to two atmospheres could be obtained. If, however, a piston filled with water is used in place of the manometer tube, a smart blow on the head of the piston-rod will almost always cause a temporary cessation of streaming, provided that the ends of the two tubes are closely approximated and connected by tightly bound

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[1] l. c., p. 29.

[2] Ewart, Journ. Linn. Soc., 1896, Vol. XXXI, pp. 563–4.

[3] Cf. Engelmann, Die Protoplasmabewegung; Hermann, Physiologie, Bd. I, Heft I; Strasburger, Jenaische Zeitschr., XII.

[4] Pfeffer, Pflanzenphysiologie, ed. I, Bd. II, p. 390; Hörmann, Protoplasmaströmung, 1898, p. 40.

pressure tubing. The stoppage may take place almost instantaneously, or may occur after a latent period of a few seconds, and similarly streaming may recommence either almost immediately or after a few seconds to a minute or more.

The simplest mode of producing a shock-stoppage is to lay a small cover-slip over the object, and then to allow a thin metal rod to fall through glass tubes of various lengths, which are held over the cover-slip but do not touch it. Or rods of different weight may be used and allowed to fall from the same height, the force of impact being then directly proportional to the mass. The magnitude of the minimal impact to cause a complete stoppage depends upon a variety of factors, such as (1) the temperature, (2) the velocity of streaming, (3) the age of the cell, (4) its previous treatment, (5) the time during which the compressing force acts.

At low temperatures a response is less readily induced than at high ones, provided these are not above 40° C. On the other hand, at the same temperature a smaller stimulus is required when streaming is fairly slow than when it has become rapid. Streaming stops more readily in young cells than in adult ones, and the stoppage lasts longer in the former case than in the latter. Previous sub-maximal stimulation of almost any kind renders the cell less responsive to mechanical stimuli. The more suddenly the force is applied, the more powerful is its action, a smart shock being much more effective than one applied more gradually. Thus if bodies of different weight are allowed to fall on the cover-slip from such heights that they have the same momentum on impact, the smaller body with the higher velocity exercises the greater shock-effect, and when it just affords a minimal stimulus, the heavier body may afford a sub-minimal one. None of these factors have previously been taken into account, and hence it is hardly surprising that widely divergent results should be obtained by different investigators or even by the same one.

A shock which is not sufficiently powerful to cause a complete stoppage may produce a more or less marked retardation, usually of short duration. A stronger minimal stimulus is required in the case of large axial cells of *Nitella* than in the smaller branch cells, provided these are of equal ages or nearly so; but if the intensity of the stimulus is made proportionate to the surface-area of the cell the reverse is the case. The same applies still more markedly to comparisons made between the end-cells and exposed medullary cells of *Chara*.

The stoppage usually almost immediately follows the application of the stimulus, but a latent period amounting occasionally to eight or even ten seconds may intervene between the two. The latter usually occurs when a nearly minimal stimulus is applied to a slowly streaming cell, but sometimes also in large cells in which streaming is fairly active. The stoppage always occurs simultaneously, or almost simultaneously, over

the entire cell, the mechanical disturbance being propagated with great rapidity in the cell-sap and directly stimulating each portion of the endoplasm, which latter responds either at once or after a latent period common to the entire cell.

The latent period of recovery varies from a few seconds to several minutes, according to the strength of the stimulus applied, the previous condition of the cell, the temperature and the supply of oxygen. After a strong shock, the recovery takes longer than after a weak one, but an increasing stimulus produces rapidly decreasing increments to the time of recovery, and ultimately no recovery at all. When streaming was previously slow, it is usually a longer time before it is active again, and the new velocity may be increased, whereas recovery is more rapid in cells which were originally actively streaming. Similarly a low temperature or a deficient supply of oxygen prolongs the latent period of recovery, which takes place, for example, more rapidly at 25° C. to 30° C. than at 10° C. to 15° C.

After several repetitions of the same shock-stoppage accommodation ensues, and the latent period of recovery may decrease from one to two minutes to 20 or 60 seconds, while if a nearly minimal stimulus is used, after ten to twenty repetitions a slightly stronger shock is required to produce a complete stoppage. A very severe shock may inhibit streaming for as long as five or rarely ten minutes, although a stoppage lasting more than five minutes is usually permanent in the case of large adult cells and indicates fatal injury.

Similar phenomena are exhibited by *Elodea* and *Vallisneria*, in which the streaming is usually secondary in origin. The cells of *Vallisneria* are readily killed by too violent a shock, while the stoppage is shorter and less easily produced when streaming has only recently become active than when it has been active some hours or days. *Elodea* is less sensitive than *Vallisneria*, and although many of the cells are killed by a shock sufficient to produce stoppage throughout the entire field, streaming may easily be stopped temporarily in single cells by locally applied mechanical stimuli. At 15° C. streaming recommences in from one to five or ten minutes, but at 25° C. in from twenty seconds to two or three minutes. In some cases the shock awakens streaming in previously quiescent cells.

A mechanical disturbance may be rapidly propagated to a neighbouring cell, and may act as an inhibitory stimulus there also, but the transference is a physical phenomenon, and hence affords no proof of the existence of plasmatic connexions between the cells, as Hörmann supposes, for in these connexions the transmission of stimuli takes place relatively slowly.

If a cell of *Nitella* or *Chara* is snipped in two, the neighbouring cells may suddenly cease to show rotation for one or two minutes. Probably

the sudden removal of the osmotic pressure on one side of each partition-wall operates as a sufficiently powerful mechanical disturbance, for as a matter of fact a suddenly removed hydrostatic or mechanical pressure does act as a temporary inhibitory stimulus to streaming. If streaming was slow in the cells adjacent to the injured one, it may become in ten to thirty minutes one and a half to twice as rapid as it was previously. This may possibly be due to the transmission of a vital stimulus by plasmatic connexions between the injured dying cell and the living ones, and the length of the latent period is such as to permit this interpretation.

The mechanical shock-stoppage is the result of an internal pulsation of the cell-sap which acts directly upon the particles of endoplasm, and either temporarily disturbs the arrangement essential for streaming, or sets up vibrations which prevent the one-sided liberation of energy necessary for its maintenance. A similar stoppage can be produced in *Chara* and *Nitella* by vibrations reaching the cell through a dense external medium (water), but not through a less dense one (air).

As regards the distinction between primary and secondary streaming in cells, Hauptfleisch[1] gives the following critical test for the latter: the first section cut exhibits streaming only after some time has elapsed, but now a second one cut from the same surface exhibits streaming immediately on examination. Suddenly applied pressure does, however, cause a temporary cessation of streaming, although Hauptfleisch denies this. Hence, the first section might show no streaming owing to the shock of section-cutting, while in the case of the second section, as the result of the first shock and recovery, a stronger stimulus might now be required to produce a stoppage. This difficulty may be partially obviated by allowing as long a time as possible to elapse between the preparation of the first and second section, and by noting the time streaming takes to commence in the first case. This latter is usually considerably longer than the latent period of recovery from a shock-stoppage, but in some cases, as Hauptfleisch himself shows, streaming begins in directly stimulated quiescent cells within five minutes (*Elodea*, *Vallisneria*, &c.), although in others not until after fifteen minutes to an hour. Even in the first case, however, temporarily inhibited primary streaming will recommence almost simultaneously over the entire preparation, whereas secondarily induced streaming will start first in the directly stimulated cells and spread slowly in regular sequence to surrounding cells, if the stimulus is sufficiently powerful and prolonged, viz. mechanical injury involving the death of certain cells. In the absence of a mechanical shock, cells bordering an injured one may be stimulated by exuded chemical products, or by the death of the connecting plasmatic

[1] Jahrb. f. wiss. Bot., 1892, XXIV, pp. 190–200.

threads. In the latter case the subsequent transmission of the stimulus must be vital, but might be the result of continued diffusion in the former case.

SECTION 31. The Action of Nutrient Substances.

Food-materials. Cells completely packed with solid food-materials never exhibit any perceptible streaming movements, and even if a tendency to streaming existed the mechanical inertia of the entire mass might be too great to be overcome by any propulsive force exerted by the relatively small protoplasmic portion. Streaming, however, often commences as the food-materials are removed. For example, streaming begins in the etiolated amyliferous winter-shoots of *Elodea*[1] after they have been kept for some days in well-aerated water at 20° C. and the starch has largely disappeared.

Similarly, the cells of bulb-scales fully charged with soluble food-materials (glucose, &c.) may exhibit no streaming until the sugar has been largely removed. The decreased internal osmotic pressure will be accompanied by a rise in the percentage of water in the protoplasm, and by a corresponding decrease in its viscosity. This, however, merely renders streaming more easy, but does not cause it. The streaming may be secondarily induced in correspondence with the fact that translocation from a cell is accelerated by the existence of streaming movements in it. Moreover, when a cellular food-receptacle is being emptied, it usually passes from a quiescent condition into a temporarily active one. When cells which exhibit streaming are starved, the movement may not entirely cease (*Chara, Nitella*) until shortly before death ensues, although in other cases a long time may intervene between the cessation of streaming and the permanent loss of vitality (*Elodea, Vallisneria*). If, when streaming has become slow in chlorophyllous cells, they are exposed to light, a rapid acceleration is usually exhibited, and the same commonly occurs when they are supplied with dilute glycerine. The addition of dilute glycerine may, however, accelerate streaming in well-nourished cells, and treatment with strong glycerine followed by subsequent washing in water causes active rotation to appear in previously quiescent leaf-cells of *Elodea*. Apparently some obscure stimulating effect is exercised which may or may not be connected with changes in the osmotic pressure, or in the percentage of water present in the protoplasm. It has already been noticed that treatment with dilute solutions of many neutral substances, including sugar, potassium nitrate, and asparagin, may accelerate slow streaming, or induce it when previously non-existent. Strong solutions of these substances,

[1] Cf. Ewart, Journ. Linn. Soc., 1896, Vol. XXXI, p. 565.

however, directly retard or inhibit streaming by increasing the viscosity of the protoplasm and decreasing the amount of energy liberated, whereas the acceleration is probably due to an indirect stimulating action.

SECTION 32. **Poisonous Substances.**

Acids. According to Dutrochet[1], although dilute acids may cause a temporary retardation of streaming in *Chara*, a complete stoppage is always permanent, whereas with dilute alkalies a temporary stoppage is readily produced. A temporary shock-stoppage may, however, be produced by suddenly immersing cells of *Chara* or *Nitella* in 1 to 2 per cent. solutions of oxalic or tartaric acid for a period of a few seconds to a minute. Recovery may occur on replacing in water. It is more difficult to do this with physiologically equivalent solutions of nitric, sulphuric, and hydrochloric acids (0·1 to ·3 per cent.), but occasional positive results show that the shock-effect is actually due to the action of the acid, and not to any plasmolytic effect. In *Elodea*, *Vallisneria*, and *Tradescantia* a temporary complete stoppage can hardly ever be produced, although pronounced retardation may occur without the power of recovery being lost.

Both organic and inorganic acids exercise a very injurious effect upon plant-cells[2], chiefly owing to the readiness with which their hydrogen ions are displaced by bases, and Klemm has shown that 0·05 per cent. solutions of HCl, H_2SO_4, HNO_3 and H_3PO_4 cause a rapid cessation of streaming in hairs of *Trianea*, *Momordica*, *Urtica*, and cells of *Vallisneria*[3]. The resistant power of different plants varies considerably; thus many fungi and the leaf-cells of Oxalis and of Crassulaceae, &c. are comparatively resistant to organic acids such as oxalic, citric, malic, &c., while many fungi are also resistant to mineral acids (HCl), though to a less degree. On the other hand, *Chara*, *Nitella* and certain Bacteria appear to be less resistant than any other plants as yet examined. Dutrochet (l. c.) found that streaming ceased in *Chara* after fifty minutes' immersal in 0·1 per cent. tartaric acid. Similarly, the addition of 0·01 per cent. phosphoric acid causes streaming in *Chara* and *Nitella* to undergo fluctuations of rapidity, the periods of retardations becoming more and more marked until streaming ceases in from half an hour to two hours. If the acid is washed away just before streaming has ceased it may in some cases regain its normal rapidity in a few minutes to an hour or so. Prolonged immersal in 0·001 per cent. or even in large quantities of 0·0005 per cent. solutions of this acid ultimately exercises a similar effect, provided the cells are free from chalk.

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[1] Ann. d. sci. nat., 1838, ii. sér., T. IX, p. 67.

[2] Cf. Fr. Schwarz, Cohn's Beiträge, Bd. V, chap. IV; Migula, Ueber den Einfluss von Säurelösungen auf Algenzellen, Breslau, 1888.

[3] Klemm, Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 685.

Elodea is less sensitive, but after twenty-four hours' immersal in 0·01 per cent. H_3PO_4 (or a shorter period in stronger solutions) streaming entirely ceases, but recommences in water in from five minutes to an hour, then slowly regaining its original activity.

Most organic acids act similarly, though not with the same vigour. Thus a 1 per cent. solution of oxalic acid corresponds approximately to a 0·05 per cent. solution of HNO_3, HCl, or H_2SO_4.[1] Streaming, for example, persists in *Trianea* for one and a half hours after the application of oxalic acid in concentrations, increasing up to 1 per cent.

SECTION 33. Carbon Dioxide and Carbonic Acid.

The presence of carbon dioxide, either as a gas or in solution, will necessarily diminish the amount of oxygen available under ordinary circumstances. Hence the poisonous character of carbon dioxide can only be correctly determined by experiments in air containing varying percentages of carbon dioxide and similar percentages of an indifferent gas, combined with experiments in which the carbon dioxide replaces a portion of the nitrogen of the air, the percentage of oxygen remaining constant. It is of interest to notice that the resistant power of different organisms varies considerably, and that as we descend the scale in both plant and animal kingdoms, we meet with organisms having great powers of resistance (Mosses, Bacteria, lower Worms, certain Infusoria[2]), together with others which are comparatively sensitive (obligately aerobic Bacteria, Infusoria, and Fungi).

The presence of a cuticle, even if thin, retards the poisonous action of carbon dioxide. Thus Kühne found that streaming ceased in hair-cells of *Tradescantia* only after forty-five minutes in pure carbon dioxide, and became active again after half an hour in air, whereas Klemm observed an almost immediate cessation of streaming when hairs of *Trianea* or leaf-cells of *Vallisneria* were suddenly immersed in CO_2, or in water saturated with this gas[3]. According to Lopriore, however, streaming does not cease until after two to three minutes' immersal in carbon dioxide in the case of hairs of *Cucurbita* and *Tradescantia*, and after it has been allowed to recommence in air it cannot be stopped again even by a current of pure CO_2 lasting for five hours. This was undoubtedly due to the fact that the gas used by Lopriore contained an appreciable quantity of oxygen, while, as Lopriore and Samassa have shown, the cuticularized hair-cells of *Tradescantia*,

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[1] Klemm, l. c., p. 36.

[2] C. Fränkel, Zeitschr. f. Hygiene, 1889, Bd. v, p. 332; Arsonval, Compt. rend., 1891, T. CXII, p. 667.

[3] Kühne, Unters. über das Protoplasma und die Contractilität, Leipzig, 1864, p. 106; Klemm, l. c., p. 36.

Cucurbita, &c., can slowly accommodate themselves to very high percentages of carbon dioxide (over 90 per cent.)[1].

A fact to which no attention has previously been paid is that sudden immersal in pure CO_2 may produce an almost immediate shock-stoppage, from which recovery is possible in air or in CO_2 largely diluted with air, but not in pure carbon dioxide. If, however, the change is a little less rapid, so that the shock-effect is avoided, the stoppage is due partly to the removal of all oxygen, but mainly to the directly poisonous action of the pure carbon dioxide.

Owing to the influence of the cuticle in retarding diffusion, the stoppage of streaming usually takes two to five, rarely ten or more minutes, in the case of hair-cells of *Tradescantia*, *Cucurbita*, *Urtica*, &c., and a shock-effect is rarely produced, whereas in *Vallisneria*, *Elodea*, *Trianea*, and in pollen-tubes, only from one to two minutes is usually required even in the absence of a shock-effect. A few plants such as *Chara* and *Nitella* are, however, inherently more resistant to the poisonous action of the gas in question. Thus streaming may only become slow in cells of these plants after from five to fifteen minutes' immersal, and may not cease until after twenty to thirty minutes. Even then rapid recovery takes place in air, slow streaming being shown in two to five minutes, active in fifteen to thirty. A similar power of recovery is possessed by the plants mentioned above.

If the exposure is prolonged as far as possible, which in the case of hairs of *Tradescantia* or *Cucurbita* may be from two to four hours, there is usually but little increase in the time streaming takes to begin in air (fifteen to ten minutes), but a considerable time, amounting to one or more hours, may elapse before it is fully active, and in some cases it remains permanently slow and ultimately ceases, death ensuing.

SECTION 34. **Alkalies.**

The action of these, on the whole, resembles that of acids. Dutrochet[2] was the first to show that sudden immersal in dilute alkalies caused a temporary shock-stoppage or retardation of streaming, followed after a longer or shorter period of renewed streaming by a progressive retardation, and ultimately a permanent stoppage. In strong alkalies an immediate permanent stoppage ensues, according to Dutrochet, although as a matter of fact, by rapid washing recovery may be rendered possible. Moreover, if the concentration is slowly increased, no shock-stoppage but only a progressive retardation is shown.

Dutrochet[3] also found that repeated changes of acidity and alkalinity

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[1] Lopriore, Jahrb. f. wiss. Bot., 1895, Vol. XXVIII, p. 531; Samassa, Bot. Zeit., 1898, p. 344.
[2] Ann. d. sci. nat., 1838, ii. sér., T. IX, p. 66. [3] l. c., p. 69.

operated more injuriously than a permanent acidity or alkalinity. For example, streaming ceased in a cell of *Chara* after nine hours in 0·1 per cent. KHO, and after one hour in 0·1 per cent. tartaric acid, whereas if the two ends of a cell were immersed in similar solutions of acid and alkali respectively, streaming ceased in five to six minutes. Similar results were obtained by the author with *Chara* and *Nitella*, the central portion of each cell being sheathed in vaseline so as to prevent the possibility of the cell forming part of an electrical circuit. A rapid stoppage occurring in from ten seconds to two minutes is simply the result of a shock-effect, as the alkaline protoplasm from one end of the cell is suddenly permeated with acid at the other. In such cases, momentary streaming may occur generally or locally, but the power of streaming is permanently lost within four to twelve minutes. More dilute solutions exercise no perceptible shock-effect, however suddenly applied, but here also a cell permanently loses the power of streaming (when its ends are in acid and alkali respectively) in $\frac{1}{10}$th to $\frac{1}{100}$th the time required when entirely immersed in one liquid. This is undoubtedly because the protoplasm is unable to accommodate itself with sufficient rapidity to the changes from acid to alkali, and from alkali to acid, whereas in either of the above media, taken singly, a certain amount of accommodation is possible.

Streaming may be completely arrested in *Elodea* and *Vallisneria* by eight to sixteen hours' immersal in 0·1 per cent. solution of normal ammonium carbonate, without the power of recovery being lost in all cases. After six to ten hours' immersal in the same strength of solution, slow creeping streaming is shown only in a few of the older cells of *Chara* and *Nitella*, and none in the younger ones. Streaming does not commence or become distinctly active until after three hours in those cells which ultimately recover, although when tested by the Bacterium method they may exhibit a power of CO_2-assimilation an hour previously in some cases, but in others still none.

After prolonged immersal in a dilute alkaline solution, the slowly streaming protoplasm usually becomes extremely vacuolated, and according to Klemm [1] the vacuoles arise, owing to the fact that the alkali converts certain insoluble constituents of the protoplasm (microsomes) into soluble and highly osmotic substances. These absorb water from the cell-sap and form vacuoles. That some such change occurs is certain, but it is not necessarily due to any direct solvent action of the alkali, for dilute solutions of caffein, which acts not as a solvent but as a precipitant [2], produce a similar vacuolation of the protoplasm. Both dilute acid and dilute alkali convert coagulable albumin into the non-coagulable acid- and alkali-albumins, but dilute acid acts on living protoplasm very differently, and

[1] l. c., p. 42.

[2] Cf. Pfeffer, Physiology of Plants, Clar. Press, 1900, Vol. I, p. 68.

causes the appearance of numerous solid granules and a rapid loss of plasticity. It is possible that this may be connected with the decomposition of basic compounds of Potassium, Calcium, Magnesium, or Iron with proteids, and the production of the corresponding salts of these metals, whereas the vacuolation produced by alkalies may be due to their liberating soluble carbo-hydrates or organic acids held in loose combination by proteid molecules.

SECTION 35. **Alkaloids.**

Dutrochet (l. c., p. 71) found that dilute watery solutions of opium caused a temporary stoppage of streaming in *Chara* within six minutes, which lasted for fifteen minutes, and was then followed by a resumption of slow streaming, ceasing after half an hour. With more dilute solutions the primary retardation or stoppage was followed by more active streaming than normal.

Caffein and Antipyrin. By using 0·1 per cent. to 0·5 per cent. solutions of Caffein, it is easy to cause a progressive retardation of streaming, and an increasing vacuolation of the protoplasm. The latter is especially well shown by the root-hairs of *Trianea*[1]. Recovery is often possible after the complete cessation of streaming in *Trianea, Elodea, Vallisneria,* &c., and more rarely in *Chara* and *Nitella,* if the stoppage is not unduly prolonged. In such cases, streaming gradually becomes active again in one to six or eight hours as the protoplasm assumes its normal appearance.

The action of antipyrin is similar in character but weaker[2]. Thus four hours' immersal in solutions of from 1 to 2 per cent. strength[3] causes streaming to cease in *Elodea* and *Vallisneria,* and to become very slow in *Chara* and *Nitella,* recovery being possible in all cases. After six to eight hours, streaming ceases in the last two plants, but recommences in water in from five to fifteen minutes, and becomes moderately active in one to two hours. After longer exposures than this, many cells are fatally affected in *Chara, Nitella,* and *Vallisneria,* and a few in *Elodea* also.

Although both caffein and antipyrin exercise a pronounced effect upon the nervous systems of the Vertebrata, they are by no means such virulent poisons as are Muscarin, Atropin, Eserin, Veratrin, and Curare, and it is of considerable interest to compare the actions of these poisons upon the nerves and contractile organs of animals, and upon the streaming protoplasm of plants. For example, Veratrin causes a nerve-muscle

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[1] Cf. Klemm, l. c., pp. 39–40. [2] Cp. Hauptfleisch, l. c., p. 221.

[3] The plants were passed through solutions of 0·1 per cent., 0·2 per cent., 0·5 per cent., and 1 per cent. or 2 per cent. strength at intervals of a few minutes. This avoids any plasmolytic shock-effect.

preparation of the frog's gastrocnemius to respond to an electrical excitation by a prolonged contraction instead of by a simple twitch. Curare paralyses the motor nerve-endings in muscle, and hence renders the latter irresponsive to nervous excitation. Muscarin (0·5 per cent.) excites the inhibitory nervous mechanism of the frog's heart, and so decreases its excitability that it ceases to beat, while Atropin (0·5 per cent.) paralyses the inhibitory mechanism, and hence causes the beat to recommence.

Muscarin. If a drop of 2 per cent. Muscarin is placed upon a cell of *Nitella* streaming almost immediately ceases, and recommences within five minutes if a drop of 2 per cent. Atropin is added. If the Muscarin is washed away as soon as streaming has ceased, it recommences in a few seconds to a minute, and is active in two to three minutes. Recovery also occurs even if the Muscarin is not removed, and no Atropin added; streaming recommencing in five to ten minutes, and being fairly active in fifteen to twenty.

The temporary stoppage is therefore due to a shock-effect, and if the Muscarin is allowed to diffuse in slowly, none is produced. Moreover, if the shock-stoppage and recommencement in water are repeated from one to a few times, streaming may become more rapid, and may no longer be stopped by sudden immersal in 2 per cent. Muscarin, although after prolonged immersal it undergoes progressive retardation. Suddenly replacing the Muscarin solution by water may cause a similar temporary stoppage, and hence the latter is due more to sudden changes in the concentration of the external medium than to any poisonous effect of the Muscarin.

Sudden immersal in dilute solutions will produce a similar effect, and, in fact, 1 and 2 per cent. solutions of sodium chloride are nearly as poisonous to *Nitella* as are similar solutions of Muscarin (1 and 2 grams in 100 cc.). Thus if a few cells of *Nitella* are placed in from 30 to 35 cc. of 0·5 per cent. Muscarin, they continue to show active streaming for several days. In 1 per cent. solution streaming slows, and permanently ceases on the second to fourth day as the cells die. In 2 per cent. solutions slow streaming may still be shown after six to twelve hours, but death ensues on the first or second day[1]. Closely similar results were yielded by *Chara fragilis* and *Chara foetida.*

The shock-stoppage is less readily induced in the case of *Elodea* and *Vallisneria*, although in 2 per cent. solutions streaming usually ceases in a few hours, death following after twelve to forty-eight hours.

[1] The plants must be gradually accommodated to the solution, for if *Nitella* is suddenly immersed in 2 per cent. Muscarin the first stoppage and recommencement may be followed within an hour either by progressive retardation, or irregular fluctuations leading ultimately to a permanent stoppage. The plant is apparently unable to accommodate itself to so sudden and violent a disturbance of equilibrium.

A 10 per cent. solution produces an immediate cessation of streaming in both cases, and the leaf-cells show signs of death within half an hour. If irrigated with 2 per cent. Atropin as soon as streaming has ceased, it begins again in three to five minutes, but the same effect is also produced after a somewhat longer interval if 2 per cent. Muscarin is used. Hence it is merely due to the dilution of the concentrated solution. Ten per cent. solution usually causes slight plasmolysis, but 5 to 6 per cent. solutions produce a similar stoppage without any perceptible retraction of the protoplast. Nevertheless, an amount of water may have been withdrawn corresponding to the elastic contraction of the stretched cell-wall, and in any case the influence of suddenly applied strong solutions is physical rather than chemical.

Dilute solutions of *Curare* gave in general similar results, but this substance appears to be more distinctly poisonous to plants than Muscarin, Atropin, or Veratrin. No precise determinations were, however, possible, the available supply of this poison being very limited.

Eserin sulphate yields closely corresponding results to those given by Muscarin, and here also sudden immersal in strong solutions (2 per cent.) produces effects which are not shown when the solution is applied in slowly increasing concentration.

If streaming in *Chara* or *Nitella* is stopped by a solution of Eserin, and dilute Atropin added as it recommences, frequently a slight temporary acceleration occurs followed in a few minutes by a retardation or temporary cessation. If the Eserin is removed by water and Atropin added when streaming is active again, the usual shock-stoppage is produced, but the latent period of recovery is shorter than before.

Atropin resembles Muscarin in its general action, but is even less poisonous. Thus a plant of *Elodea* remained living for three weeks although kept in a sterile 2 per cent. solution of Atropin renewed every two or three days.

Cells of *Nitella* and *Chara* may remain living and showing fairly active streaming from four to seven days in solutions containing 0·5 per cent. Atropin and 0·5 per cent. Muscarin, whereas in 1 per cent. solutions of either of these substances, the cells are usually killed within two to four days. This does not indicate any such antagonism as is shown when these poisons act simultaneously upon the nervous mechanism of the Vertebrate heart, for plants may withstand the action of various poisons when applied conjointly, each in half the lethal concentration.

Veratrin[1] is insoluble in water, but dissolves readily in alcohol. By dilution with water, solutions may be obtained containing 1 per cent. of Veratrin and 2 to 3 per cent. of alcohol. Such a solution causes the

[1] Obtained pure from Merck of Darmstadt.

usual shock-stoppage, often followed by a temporary acceleration, and a subsequent progressive retardation, which in the case of *Nitella* and *Chara* ends in a permanent stoppage in one or two hours. The temporary acceleration may be due to the presence of the alcohol, and the rapid fatal effect is partly due to the fact that alcoholic solutions of Veratrin are slightly alkaline[1].

Veratrin nitrate is soluble in water, and a neutral solution containing 1 per cent. of Veratrin in the form of the nitrate caused an immediate stoppage of streaming in *Chara* and *Nitella*, lasting for eight to fifteen minutes, if the solution was not removed. If streaming was still absent after five to ten minutes, the addition of water usually caused an immediate recommencement. After the stoppage in Veratrin and recommencement in water have been repeated a few times, the latent period of recovery in 1 per cent. solution of Veratrin nitrate becomes much shorter.

After two hours' immersal in the 1 per cent. solution, streaming is distinctly slower in cells of *Nitella*, but may still be present after four to eight hours if the cells have been gradually accommodated to the solution. Streaming permanently ceases and death ensues after ten to twelve hours in 1 per cent., and after sixteen to twenty-four hours in 0·5 per cent. neutral Veratrin nitrate solution.

Elodea yields similar results in solutions of three times greater concentration. Slow streaming may still be present after twenty-four hours in 1 per cent. solution, but after three days in 1 per cent. and after five to seven days in 0·5 per cent. solution all the leaf-cells are dead[2].

None of the above substances, therefore, appears to be specially poisonous to the plants examined, and in addition sunflower, cucumber, and maize seedlings can withstand repeated watering with dilute solutions, and continue to grow when their roots are immersed in nutrient solutions containing 0·1 per cent. of the substances in question, although not quite so rapidly as in normal media. Moreover the plants which produce these poisons must be indifferent to them. Indeed various fungi (*Penicillium glaucum*, *Penicillium sp.*?), saprophytic bacteria (*Micrococci*, *Bacilli*), as well as flagellate Infusoria, such as *Monas* and *Bodo*, will develop with fair rapidity in plant decoctions containing 1 per cent. and 0·5 per cent. solutions of Atropin, Eserin, and Muscarin. *Penicillium* will even grow slowly on 1 per cent. and 0·5 per cent. solutions, to which only inorganic salts have been added, the alkaloids acting here not as poisons but simply as bad nutrient materials.

A very important point to determine is whether these poisons actually

[1] The solutions of Atropin, Eserin sulphate, and Muscarin exhibited an extremely faint acidity (Grübler's preparations).

[2] The solutions must be renewed daily, since plants of *Elodea* slowly remove the nitric acid from Veratrin nitrate, causing Veratrin to be precipitated.

penetrate the protoplasts. This must of course occur in the case of *Penicillium*, &c., unless the alkaloids undergo extracellular digestion and are absorbed as other substances. The permanence or non-permanence of plasmolysis cannot be used as a test for absorption or non-absorption, since sufficiently strong solutions to cause plasmolysis rapidly kill the cells. After prolonged immersal in 2 per cent. solutions, the osmotic pressure of the cell may be slightly higher than before, but this might easily be the result of an attempt at accommodation by increasing the percentage of soluble substances in the cell-sap, and affords no proof that the 2 per cent. solution diffuses slowly through the protoplasm.

It has already been mentioned that plants such as *Elodea*, &c. withdraw nitric acid from a solution of Veratrin nitrate in water, causing the Veratrin to be precipitated. This is because the nitric acid is used in metabolism, but apparently not the Veratrin. The precipitate is mostly extracellular, but occasionally the cell-sap of cells of *Elodea* and *Trianea* becomes cloudy after long immersal in a dilute solution, and the cloudiness is due to minute particles resembling those formed in the external fluid. These particles dissolve again in dilute nitric acid, and disappear for the most part when the living cell is treated with dilute alcohol. Hence they are presumably composed of Veratrin, and the latter must penetrate the protoplast slowly in the form of Veratrin nitrate, although the very fact that it may accumulate in the cell-sap shows that it is not retained by the protoplasm.

In no case does the permeability of the plasmatic membranes of cells containing coloured cell-sap appear to be affected by dilute solutions of Muscarin and Atropin, as long as they remain living. The escape of the coloured sap is always a sign that the cell is fatally affected, and is, in fact, usually a post-mortem phenomenon. Similarly in cells killed by acids or alkalies, turgor is almost always maintained up to death, and if the action is at all rapid, the cells are fixed in an uncontracted condition.

SECTION 36. Alcohols.

Dutrochet[1] observed that dilute alcohol ($\frac{1}{20}$ of 36°) caused a temporary retardation of streaming in *Chara*, followed by a subsequent acceleration to above the normal velocity. Both ethyl- and methyl-alcohol produce this result on *Chara*, *Nitella*, *Elodea*, *Vallisneria*, and *Trianea*, in concentrations of not more than 1 to 2 per cent. strength. If the alcohol is gradually applied, the first retarding effect, which is the result of shock, is not shown, and only the accelerating influence is manifested.

Above this strength of solution a retarding influence is shown, which

[1] l. c., p. 72; cf. also Klemm, l. c., p. 44.

progressively increases until an almost immediate stoppage of streaming and coagulation of the protoplasm ensues. Theoretically there should be a percentage of alcohol which leaves streaming unaffected, but as a matter of fact, even when gradually applied, a strength of solution which causes at first an acceleration (2 to 5 per cent.) may ultimately produce a retardation, while a solution strong enough to cause no acceleration produces a progressive retardation.

The retarding influence of strong alcohol is easy to understand, being mainly the result of the withdrawal of water, but the accelerating influence of dilute solutions appears to be due to a direct chemical action on the protoplasm. Dilute glycerine also directly accelerates streaming, strong glycerine retarding or stopping it. An indirect stimulating effect may be exercised in some cases, as when treatment with strong glycerine and subsequent washing in water cause streaming to appear in previously quiescent cells.

Both alcohol and glycerine rapidly penetrate the protoplasm, but since alcohol has nearly the same viscosity as water[1], while that of glycerine is very much greater, the acceleration of streaming can hardly be due to any direct change of viscosity produced by their mere presence. An indirect effect upon the viscosity of the protoplasm is quite possible, although more probably both of these substances exercise some chemical effect, causing either a general increase of katabolism, or a greater liberation of the kinetic energy utilized in streaming. Alcohol and glycerine both exercise a pronounced influence upon animal metabolism, the former accelerating katabolism, while the latter increases the production of glycogen by the liver.

SECTION 37. **Anaesthetics.**

Kühne[2] was probably the first to show that chloroform and ether arrest streaming. Very dilute solutions of ether at first slightly accelerate streaming, and it is interesting to notice that the inhalation of ether acts at first as a nervous excitant upon animal organisms. Solutions in water of from 10 to 25 per cent. saturation of both chloroform and ether at once retard streaming, and ultimately cause it to cease without any temporary quickening preceding death, as often occurs in other cases. If, however, the action is not unduly prolonged, on returning to water the streaming may become for a time more active than it was before, whereas a continuance of the previous retardation usually indicates that the cell has been fatally affected. Hauptfleisch (l. c., p. 220) has shown

[1] When alcohol is added to water, the viscosity increases.

[2] Unters. über das Protoplasma, 1864; cf. also Klemm, l. c., p. 54, Repr.; Overton, Studien über die Narkose, 1899.

that treatment with dilute chloroform followed by washing in water will usually cause streaming to appear in cells which have a tendency to this form of activity. Both chloroform and ether probably enter into loose union with certain of the constituents of the protoplasm, and their action upon streaming is simply the result of their general action upon metabolism.

SECTION 38. Metallic Poisons.

As in the case of acids and of such substances as sodium and calcium chlorides in which the acid ions seem to play the poisonous part, all concentrations sufficient to produce any effect cause from the outset progressive retardation, which may be preceded by a temporary shock-stoppage if the poisonous solution is moderately concentrated and suddenly applied.

Dilute solutions of sodium chloride are comparatively innocuous to most plants, and indeed the presence of this salt forms one of the conditions for the development of most marine algae. Plants of *Chara* and *Nitella*, however, which had been kept for some time in nearly pure water, ceased to show streaming, and ultimately died in solutions containing from 0·1 to 0·5 per cent. of salt. That this is a toxic effect is shown by the fact that partial plasmolysis occurred only in 2 per cent. solutions. With regard to copper sulphate, which, according to Nägeli[1] acts as a powerful poison in excessive dilution, apparently contradictory results to those of Nägeli have been obtained by Klemm and by the author. Klemm (l. c., p. 43) found that hairs of *Momordica* still exhibited weak streaming after an hour in 10 per cent. $CuSO_4$.[2] The same is the case with hairs of *Cucurbita*, with hairs of *Trianea* in 2 per cent. and with *Chara* and *Nitella* in 0·5 per cent. solutions. In all cases the $CuSO_4$ appears to penetrate the protoplast, and in *Momordica* and *Trianea* it accumulates in the cell-sap by a process of passive secretion.

The explanation of the temporary resistant power is that (1) the full poisonous action is only slowly exercised ; (2) the relative percentages of free ions to dissolved salt are less in concentrated than in dilute solutions ; (3) the salt acts as a cumulative poison, so that a subminimal external percentage may accumulate slowly internally until the poisonous percentage is reached. This is shown by the fact that large masses of *Chara*, *Nitella*, or *Spirogyra*, are unaffected by immersal in small quantities of 0·01 per cent. $Cu\,SO_4$, whereas in large quantities of the same solution they die in from one to a few days.

Penicillium is able to grow upon nutrient solutions containing 5 to

[1] Oligodynamische Erscheinungen, 1893 (Denkschr. d. Schweiz. Naturf.-Ges.), Bd. XXXIII.

[2] The presence of a cuticle naturally diminishes the amount of poison penetrating the protoplasm in unit time.

10 per cent. of copper sulphate, owing to the fact that the ectoplasmic membrane of this plant is impermeable to the salt in question, but this appears to be an exceptional case[1].

The action of a metallic poison is markedly influenced by temperature, the minimal poisonous dose being lower at a high temperature than at a low one, even when a small range of temperature is used, 5 to 10° C., 15 to 20° C., 25 to 30° C. This is because metabolism is more active at the higher temperature, and hence the interference of the poison is more pronounced. For this reason also, the time of exposure necessary to produce a fatal effect is much shortened at the higher temperature. If the effects at 15 to 20° C. are compared with those at 30° C. to 40° C. the difference is still more pronounced. This is partly due to the increased dissociation at the higher temperature, and hence the larger percentage of the free ions upon which the poisonous action depends.

SECTION 39. **Electrical Stimuli.**

Becquerel and Dutrochet[2] were the first to show that an electric current caused a temporary stoppage of streaming in *Chara* and *Nitella*, the result being dependent on the strength of the current but not upon its direction. Jurgensen[3] found that weak currents caused a retardation and ultimate complete stoppage of streaming in *Vallisneria spiralis*, and that stronger currents produced an immediate permanent cessation. Kühne[4] observed in the case of hairs of *Tradescantia* exposed to constant currents that the protoplasm accumulates at the positive pole, and that owing to electrolytic action the cell-sap at this end turns red and acid; but, at the negative end, alkaline and green. He also noticed that under the influence of induction shocks the protoplasm aggregated in masses or balls, from which condition recovery was possible.

Velten[5] found that weak induction shocks or weak constant currents caused a retardation of streaming, and that after the latter had nearly ceased under exposure of very limited duration, from one to two hours were required for complete recovery.

Klemm (l. c., pp. 24 seq.) has shown that the nucleus is killed first, as is evidenced by its swelling and absorbing pigments, while the large vacuolated masses into which the protoplasm separates may exhibit streaming for as long as four hours, although they contain no nucleus. Similarly streaming may continue after the nucleus has been killed.

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[1] Cf. Pfeffer, Pflanzenphysiologie, 2. Aufl., Bd. II, p. 342.

[2] Ann. sci. nat., 1838, ii. sér., T. IX, p. 80.

[3] Stud. des physiol. Inst. zu Breslau, 1861, p. 87. Cf. also Sachs, Physiologie, pp. 74 seq., for the works of Brücke, Heidenhain, &c.

[4] Unters. über das Protoplasma und die Contractilität, Leipzig, 1864.

[5] Sitzungsb. d. k. Akad. d. Wiss. zu Wien, 1876, Bd. LXXIII. I, p. 350.

Corresponding observations were previously made by Velten [1]. According to Klemm the inner plasmatic membrane is destroyed before the outer, and in the last stage of disorganization the protoplasm swells and becomes highly vacuolated. This is because the action of the electricity is such as to cause various solid substances to become soluble and dissolve. These phenomena are not, however, connected with streaming or with the presence of oxygen, for they are produced in the absence of the latter, and also in chloroformed cells.

Hörmann [2] investigated more exactly the phenomena of electrical excitation, and more especially the internal electrical changes which follow stimulation. The experiments were performed exclusively with *Nitella*, and by laying the cells across insulating strips of vaseline and using non-polarizable electrodes, Hörmann made certain that the whole of the current passed through a portion at least of the cell, and that no other effect than the electrical one was produced upon it. This use of vaseline is to be recommended in all cases in which the objects are of sufficient size, except when the conjoint effects of thermal and electrical stimuli are being investigated.

Hörmann found that after the stoppage of streaming by the application of a galvanic current had been repeated once or twice, a weaker current sufficed to produce the same effect. This he ascribes to an increased excitability of the cell, and states that ultimately it becomes wearied and responds less readily. Dutrochet and Becquerel (l. c., p. 38) observed that streaming might recommence in *Chara* while the current was still passing, and that a decrease or break of the current caused another temporary stoppage. Those results have been extended by Hörmann, who finds that in *Nitella* a weak current produces a temporary stoppage over the entire cell after a latent period of one to seven or eight seconds, whereas with strong currents, at *make* streaming temporarily ceases at the kathode, and remains slower there all the time the current is passing (katelectrotonic excitation). On breaking the circuit, a temporary stoppage occurs at the anodal end only. Hence, according to Hörmann, the production of katelectrotonus and the disappearance of anelectrotonus constitute stimuli exciting a stoppage of streaming just as they do in producing a contraction in muscle-fibre. With weak currents the katelectrotonic and anelectrotonic excitations spread over the entire cell, whereas strong currents diminish the excitability at the anode on making the circuit, and at the kathode on breaking it. Hence the stimulus is confined to the kathode in the first case and to the anode in the second.

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[1] Bewegung und Bau des Protoplasmas. Flora, 1873, p. 122.
[2] Protoplasmaströmung bei den Characeen, Jena, 1898.

That the time factor should be of importance when the electrical stimulus is nearly minimal might be expected; a momentary weak current producing no perceptible effect. In the case of induction currents, it is only natural that the stronger secondary current at 'break' may act as a minimal stimulus, when the weaker 'make' current affords a sub-minimal one.

Using a Lippmann's capillary electrometer, Hörmann was able to show that a stoppage, whether produced by induction shocks or by a sudden local fall of temperature, is accompanied or preceded by an electrical disturbance which travels around the cell in the form of a wave, and corresponds to the 'negative variation' of animal physiology. Since the wave may precede the stoppage it cannot be the direct result of it, but is probably due to a chemical disturbance which is propagated through the cell, and acts as the stimulus inhibiting streaming.

From these facts Hörmann concludes that a stoppage of streaming in *Nitella* is fundamentally the precise counterpart of a contraction in a muscle-fibre, and that the different response is due to some essential difference of protoplasmic structure. This last deduction is by no means a correct one, for a difference in the character of the response may be due to a difference in the manner in which the stimulus is received by the percipient organ. Thus given a slight difference in the construction of the steam-cock (percipient organ), the same movement of the hand (stimulus) may cause one steam-engine to be suddenly arrested, and the other to move rapidly forwards, although both have otherwise precisely similar constructions (motor-mechanisms). Moreover there are several fundamental differences between a stoppage of streaming and a muscular contraction. Thus in the first case less energy is consumed and less work done than before, while the shape of the protoplasmic contents remains under minimal stimulation the same as before. In the second case more energy is consumed and work done than in the resting condition, and the external shape of the protoplasmic contents of the muscle-fibre or muscle-cell always undergoes a pronounced change. This latter difference is partly due to the presence of a relatively rigid cell-wall in plants, for under maximal stimulation plant-protoplasts also exhibit a change of shape.

It must always be remembered that the negative variation is the result of differences of electrical potential, produced probably by chemical changes propagated in the form of a wave, and it does not necessarily follow that these chemical changes are always precisely similar in character, and always act in a similar manner upon the irritable protoplasm. The very fact that the rate of propagation varies enormously in nerves, muscle-fibres, and plant-cells or tissues is almost conclusive proof that dissimilar 'explosive' or specifically differentiated conducting substances are concerned in the different cases.

In spite of these numerous and exhaustive researches many points of interest still remain to be solved not only as regards the direct and the after-effects of electrical excitations, but also concerning the conjoint effects of electrical and other stimuli. For purposes of experimentation cells of *Chara* and *Nitella* and strips of leaf-cells of *Elodea* and *Vallisneria* were mainly employed. In estimating the sensitivity to electric currents account must always be taken of the sectional area the current traverses, even when the passage of the whole of it through the experimental object is ensured by vaseline insulations. When this is done it can easily be seen that *Nitella* is more sensitive than *Chara*, *Chara* than *Vallisneria*, and *Vallisneria* than *Elodea*; from six to twelve times the intensity of current necessary to produce an immediate stoppage of streaming in *Nitella* being required to produce the same effect in *Elodea*, if applied with corresponding suddenness.

Jurgensen[1] states that the current from one Grove cell produces no perceptible effect on streaming in *Vallisneria*, that from two to four cells a retardation and ultimately a permanent stoppage, and that from thirty Groves an immediate permanent cessation. These figures are, however, much too high if strips of leaf-cells are used, and the whole of the current passes through them. The true shock-stoppage is, however, usually merely temporary, and its non-observance by Jurgensen was probably due to the fact that the currents used by him did not gain their full strength instantaneously. Occasionally, it is true, when streaming is very active in cells of *Vallisneria* and *Elodea*, comparatively strong currents may only cause a temporary retardation, and still stronger ones may cause either a permanent stoppage, or a temporary one followed after a period of slow streaming by a permanent cessation.

In producing a shock-stoppage the rapidity with which the current attains its maximal strength is of great importance. This can easily be shown by interposing in the circuit long insulated coils of wire immersed in water, and increasing the voltage of the battery so as to give the same strength of current as before. Under such circumstances a certain strength of current may act as a sub-minimal stimulus, although when the same strength of current is suddenly applied in a free circuit of low resistance a shock-stoppage may be produced. The current must also act for an appreciable fraction of time such as a quarter or a half of a second, and under such conditions $\frac{1}{10}$th to $\frac{1}{20}$th of the current from a standard Daniell's cell may suffice to cause a shock-stoppage in *Nitella*. If, however, a very weak current is slowly increased in strength by moving the slider of a rheochord, the stoppage usually only occurs with currents of distinctly greater intensity, provided that the increased excitability resulting from

[1] Stud. d. phys. Inst. zu Breslau, 1861, Heft 1, p. 38.

the previous sudden excitation is allowed to pass away before the slowly increasing current is applied. These results therefore confirm those obtained by Hörmann in a somewhat different manner (l. c., p. 63).

Weak currents frequently accelerate streaming both as a direct effect and as a transitory after-effect. The acceleration is especially noticeable when streaming was previously slow. After such currents have been passing for one or more hours, a secondary retardation usually becomes manifest, and this leads ultimately to a permanent stoppage and death. Frequently, however, temporary spasmodic accelerations of streaming are shown until just before the final stoppage and death.

After a weak constant current has been passed through a cell for some time, it becomes less sensitive owing to accommodation or fatigue, and may now not show any direct response to a current of treble the intensity of one which previously caused a temporary shock-stoppage. The sudden cessation of a constant current may also cause a shock-stoppage, and this, according to Hörmann, is owing to the disappearance of the anelectrotonic condition at the anode constituting an excitation.

SECTION 40. Constant Currents at varying Temperatures.

The plant-cells were placed in a hot chamber on the under side of a cover-slip in a minimal quantity of water, and were laid across two greased lines on the cover-slip. At these points the water does not adhere, and hence the whole current used passed through the cell examined, which lay between the electrodes but not actually upon them. The platinum electrodes were sealed to the wires within small glass tubes entering the hot chamber through the metal tubes provided for the entry and exit of gases. The appended figure represents a simple arrangement suitable for demonstration if provided with a rheochord or coils of resistance wire[1]. For accurate experiments a galvanometer and shunt are required.

An electrical stimulus which is sub-minimal at a low temperature may suffice to produce a shock-stoppage at a higher one. This applies in general to temperatures lying between 10° C. and 40° C.; above and below these limits a stronger current being usually required, the cell being less readily excitable. The latent period of recovery on the other hand steadily decreases as the temperature is raised from 0° C. to from 36° C. to 45° C., above which temperatures it rapidly increases to infinity. This effect of temperature is best shown when a sub-maximal stimulus is used and allowed to act for a regulated period of time (two to ten seconds).

[1] In accordance with the general law concerning the influence of temperature on the electrical conductivity of electrolytes, the resistance of the filament decreases slightly as the temperature rises, and hence the current traversing it increases correspondingly, but if care is taken that the external resistance is at least 100 times that of the heated portion the error becomes insignificant.

In illustration the following table giving the averages of four experiments with *Nitella translucens* is appended; the times of flow across a measured

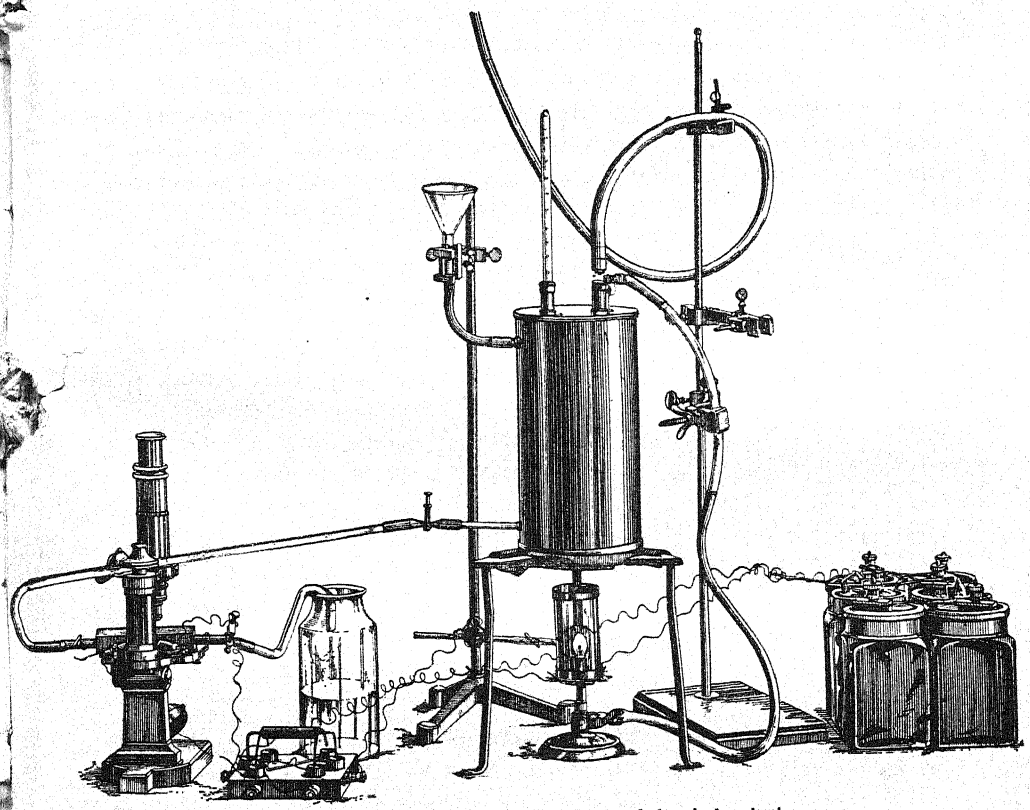

FIG. 10. Apparatus for showing conjoint thermal and electrical excitation.

portion of the field being noted before and after the application of a constant current lasting for five seconds.

Temperature.	Original time of flow.	Latent period of recovery after stimulation.	Streaming moderately active in	Nearly normal in	Above normal in
20° C.	9·5 secs.	3 min.	5–6 min.	10 min.	15 min.
30°	7·5 ,,	1·5 min.	3 ,,	5 ,,	8·5–9 secs.
40°	5·5 ,,	45 secs.–1 min.	2 ,,	5 ,,	10 min.
45°	5 ,,	50–60 secs.	2·5 ,,	6 ,, at 40° C.	7 secs.
at 45° C. for 15 min.	8 ,,	1·6–2 min.	5 ,,	10–15 min. at 40° C.	
50° C.	4·5 ,,	1–1·5 min.	5 ,, at 40° C.	10 min. at 40° C.	
at 50° C. for 15 min.	11·5 ,,	No recovery			

Above 40° C. the result produced differs according to the duration of the previous exposure to the high temperature. It is worthy of note that although the strength and duration of the current influence the length of

the latent period of recovery, they do so to a very incommensurate extent, and the period seems sometimes to fluctuate independently of them.

Similar results were obtained with *Chara*, *Vallisneria*, and *Elodea*, except that these plants, and especially the last named, are able to withstand somewhat higher temperatures.

The direct effect of a constant current is to lower the optimal and maximal temperatures for streaming, so that at low temperatures the action of a weak constant current is usually to accelerate streaming. Stronger currents, however, retard it from the outset, and hence antagonize the accelerating influence of a rise of temperature. In this case streaming is more rapid under the conjoint influence of a moderate rise of temperature and of a moderately strong current, than when the latter only is applied, but is slower than when only the rise of temperature comes into play. If currents are used which cause only a temporary shock-stoppage, or none at all when slowly applied, the usual effect is to lower the maximal temperature by from 4 to 5° C. with short periods of exposure. But if stronger currents are used and the duration of the exposure prolonged, streaming may ultimately cease as much as 10° C. below the usual maximal point (viz. 40–44° C. instead of 46–52° C.), although when exposed to similar currents the same length of time at from 18–25° C. streaming remained active, and in some cases became even more active than before.

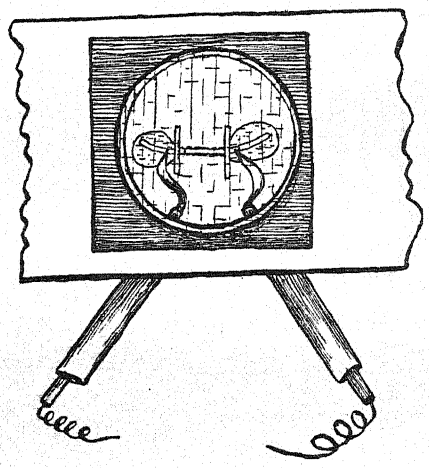

FIG. 11. Hot stage arranged for electrical excitation.

SECTION 41. **Induction Currents.**

Induced alternating currents gave similar results, except that the immediate action is more marked owing to the greater intensity of the currents and their more rapid rise and fall. Weak induction shocks cause slow streaming to become more active, and may excite it in *Elodea* and *Vallisneria*. Strong induction shocks cause in all cases a temporary or permanent stoppage. As the temperature rises to from 35° C. to 40° C., the recovery and recommencement of streaming take place more rapidly, but above these temperatures more slowly, in spite of the steady increase in the respiratory activity.

Similarly as the temperature rises above 20° C. the minimal intensity for a shock-stoppage is lessened, so that the primary and secondary coils

may be moved further and further apart. This can best be shown by applying the single induction shock produced on breaking the circuit. Above 40° C. a stronger shock is usually required, that is the sensitivity is decreased, and the latent period of recovery becomes longer. Below 15° C. an increased stimulus is also required, and the latent period of recovery at 5° C. to 10° C. is usually much longer than at 15° C. to 25° C.

In addition to the latent period of recovery, there is also a latent period of response between the application of the stimulus and the stoppage of streaming, however powerful the former may be. This latent period of response varies from one-half to ten seconds or even more, and is influenced by (1) the age, condition, and size of the cell; (2) its previous treatment; (3) the temperature. It is longer in old, large, well-nourished cells, and it is shortened by rises of temperature up to but not above 36 to 40° C., by slight starvation, and by previous sub-maximal stimulation.

SECTION 42. **Electrolytic Action.**

After strong induction currents have been passed for a short time through a cell of *Nitella* or *Chara* laid across platinum electrodes, a browning of the cell-wall is often observable, especially near to the positive electrode. This may appear before or after the cell has been killed and streaming has ceased. It is an electrolytic effect due to the algebraic sum of the stronger 'break' shocks (+), and the weaker 'make' ones (−), being a positive quantity. If, however, the induced currents at 'make' and 'break' are nearly equalized by using the Helmholtz side-wire arrangement, no such effect is produced, even when the primary current is increased so as to give approximately the same strength to the secondary currents.

The electrolytic effects of constant currents have been frequently described (cf. Kühne, l. c.), and they form a very disturbing factor in prolonged experiments upon excitability. The fatal action of weak but prolonged currents is almost entirely due to their disorganizing electrolytic action upon the protoplasm, and Klemm (l. c., pp. 56–62) has shown that various solid constituents both of the nucleus and of the cytoplasm are rendered soluble. This causes both these structures to swell and become highly vacuolated. For such action a certain voltage is essential, but a current small in quantity needs only to act for a longer time to produce the same total effect as a stronger one of limited duration. The injurious action is less pronounced when the effect of external electrolysis is eliminated by separating the cell from each electrode either by an intervening cell or by a few millimetres of water. The internal electrolytic effect can, however, only be suppressed by the use of alternating currents of equal strength, for the cell is composed of substances having dissimilar electro-motive and electrolytic properties.

SECTION 43. Conductivity and Resistant Powers of the different parts of the Cell.

Living protoplasm appears to offer a somewhat greater resistance to the passage of an electric current than dead 'protoplasm,' a conclusion arrived at by Kühne (l. c.) from *a priori* reasoning, without experimental proof. The latter can be obtained by passing a weak current of low voltage through a Wheatstone bridge arrangement, one section of which includes a filament of *Chara* or *Nitella*. On killing the cells by touching them with a hot wire or by applying powerful induction shocks, the galvanometer after a temporary disturbance remains permanently deflected in such a manner as to show that an increased current is passing through the filament, i. e. that the resistance of the filament has decreased. The deflection attains a maximum in from a few minutes to an hour after the cell has been killed, then usually slowly diminishing as the cell-sap exudes from the cell and the protoplast retracts. The decreased resistance is apparently correlated with the change from the condition of a viscous liquid to that of a solid, i. e. with the coagulation of the protoplasm[1]. The same effect is produced when the heated wire is applied to the ends of the cells lying beyond the electrodes, and hence out of the path of the current, and the same is also the case when the cells are treated with dilute HCl (2 per cent.) for thirty seconds, and then rapidly washed with water.

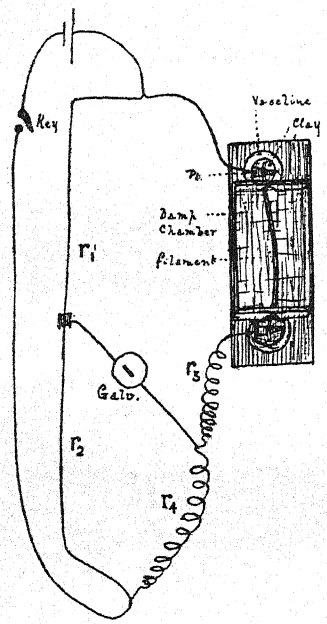

FIG. 12. To show change of resistance on death. The resistance r_3 prevents the passage of strong currents through the filament during adjustment. The Pt electrodes rest on white clay in contact with the ends of the cells which are covered on top by vaseline.

If a filament of three cells is stimulated, it will be found that to produce a shock-stoppage requires a stronger current when the two end cells are living than when they have been killed. The two experiments must, however, always occur in the order given, and hence it is possible that a previously sub-minimal stimulus may become an operative one, not because the resistance of the filament as a whole has decreased so that more of the current flows through it, but because the excitability has been increased by the previous stimulation. Both factors are probably opera-

[1] See Appendix (Influence of Coagulation on Conductivity).

tive, for if a high resistance is interposed in the circuit and a stronger battery used, the same strength of current may be obtained without the small changes in the resistance of the filament being able to affect the strength of the current perceptibly. When this is done a similar though less pronounced difference between the currents required for a shock-stoppage is usually, though not always, shown. Hence the readier response is not solely due to an increased excitability, but also to the diminished resistance.

The electrical conductivity of the different parts of the cell is certainly not the same, the cell-wall when moist and uncuticularized, and the cell-sap appearing to conduct best, and the protoplasm less readily. Hence in long cells with a thin lining layer of protoplasm most of the current will pass through the cell-sap, but in tissues composed of rounded protoplasmic cells relatively more of the current will pass through the cell-walls. The cell as a whole appears to have a lower electrical resistance than the water outside it. This may be shown by placing a glass tube containing tap-water in circuit with a galvanometer, and deflecting through the circuit a fraction of the current from a single cell. The galvanometer may show little or no deflection, but if filaments of *Nitella* or *Chara* are placed across the platinum electrodes in the glass tube a distinct deflection is shown, and hence the external resistance in the circuit has been decreased. The same can be shown by the Wheatstone bridge arrangement previously mentioned. The fact that a pronounced electrolytic effect may be produced both upon the cell-wall and upon the cell-sap, before streaming has ceased in the protoplasm, points to a lesser conductivity in the latter.

When a current is passed through a cell in which the nucleus is anchored to the wall by threads of protoplasm, the threads and the nucleus are always affected first. The threads become thicker and are retracted, while the nucleus first swells strongly and then ultimately collapses and dies, although streaming may in some cases continue for one to several hours if the current is then removed. This may partly be due to the greater sensitivity of the nucleus to electric currents, but is also probably due to the fact that since it and the threads lie in the better-conducting cell-sap they are exposed to more of the current and experience a greater electrolytic action than the peripheral layer of protoplasm. That an inherent difference between the resistant powers of the nucleus and cytoplasm does actually exist, can however be shown by using cells (*Elodea, Vallisneria, Urtica*) in which the nucleus usually lies in the peripheral cytoplasm. Here, also, the collapse and death of the nucleus occur before the whole of the cytoplasm has been fatally affected (turgor still present), or sometimes before streaming has ceased.

Klemm has shown that the endoplasmic (vacuolar) membrane frequently bursts or collapses before the rest of the cytoplasm is killed, and this may be due to its immediate contiguity with the better-conducting

cell-sap. The ectoplasmic membrane is, however, often the last part of the cell to die, and this is probably due to its having acquired a greater resistant power to external agencies, in adaptation to its more exposed situation and more changeable environment.

If cells are subjected to very weak currents[1] for prolonged periods of time, the course of events may be slightly different, for the endoplasm of cells of *Chara* and *Nitella* may still show slow creeping streaming after the ectoplasm has shown signs of being fatally affected, such as partial local retraction, irregular arrangements of chloroplastids, and appearance of gaps between them, collapse of chloroplastids, and protrusion of the contained starch grains. The cells then showed no power of CO_2-assimilation when examined by means of the Bacterium method. In such cases the order of death appears to be (1) nucleus, (2) ectoplasm, (3) ectoplasmic membrane, (4) endoplasmic membrane, and (5) endoplasm, whereas with stronger currents the order appears to be in the uninucleate cells of *Tradescantia, Urtica, Trianea*, &c., (1) nucleus, (2) endoplasmic membrane, (3) endoplasm, (4) ectoplasm, (5) ectoplasmic membrane.

Streaming may often persist after the power of CO_2-assimilation has been temporarily or permanently lost. On the other hand, according to Kny[2], after passing a 60 volt constant current, or induction currents giving a 2 cm. spark, through cells of *Nitella* and *Spirogyra*, an active power of CO_2-assimilation could be detected in them by the Bacterium method for one to three days afterwards, although streaming had permanently ceased, the chloroplastids become disorganized and the protoplasts retracted. Kny indeed concluded that the effect of very strong electric currents was to increase the assimilatory activity of the chloroplastids, although killed, altered in shape, and more or less completely disorganized. It seems, however, hardly possible that a vital function could continue with increased activity in a dead cell, and, as a matter of fact, these remarkable results were due to the use of impure cultures and unringed preparations. The dying or dead cells evolve nutritious substances which attract facultatively anaerobic Bacteria, and even aerobic ones in the presence of traces of oxygen derived from without. In no case does a dead cell, when properly tested, exhibit the faintest power of CO_2-assimilation[3].

It is not impossible that weak constant currents may increase the activity of CO_2-assimilation in living cells, either directly or as an after-effect. No positive results have, however, been obtained as yet, and certain observations of my own point to the contrary conclusion.

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[1] A current of unit-voltage may fatally affect a cell of *Nitella* in from a few minutes to half an hour, if the external resistance is low, and one of 2 to 3 volts in less than a minute. Stronger currents are required with leaves of *Elodea* and *Vallisneria* unless strips of leaf-cells are employed.

[2] Ber. d. deut. bot. Ges., Bd. XV, p. 399.

[3] Ewart, Bot. Centralbl., 1898, Bd. LXXV, No. 2.

Cells laid upon the positive electrode may, if dead, evolve electrolytic oxygen for a short time after the current has ceased, but this is a purely electro-chemical phenomenon, and in living cells this oxygen is absorbed by the protoplasm, and hastens its death.

SECTION 44. The Influence of the Direction of the Electrical Current.

Elfving[1] found that when a fairly strong electric current passes longitudinally through a root, growth is retarded, and that most markedly when the direction of the current is opposed to that of growth. Weaker currents, however, yield negative results[2], and we may safely regard the positive results as being due to the electrolytic action of the stronger current, the electrolytic ions liberated at the anode acting more injuriously upon the growing apex than those liberated at the kathode. It must, moreover, be remembered that the electrolytic effect is not confined to the electrodes, but may take place at every point in the path of the current at which it passes from a conducting medium to an electrolytic solution, or even from one electrolytic solution to another, if these are dissimilar and of restricted distribution. The ions of water, and of all salts uniformly permeating the plant, will appear mainly at the electrodes, but any electrolytic substance present in a particular cell only will be electrolyzed in that cell, and its ions will appear on the opposite sides of the cell. The action is the same as when a current is led in series through solutions of gold, silver, and copper, all of which it decomposes simultaneously.

Recent investigations[3] have shown that when a weak current passes transversely through roots growing in soil, it apparently accelerates their growth, but this is probably owing to the influence of the current in accelerating the solution and absorption of the insoluble food-constituents present in the soil. In any case, it seemed of interest to determine whether any relation exists between the direction of streaming and the action of the current. Velten[4] has shown that electrical currents affect streaming equally, whether in the same or in the opposed direction, although in dead cells filled with floating particles, a fictitious streaming may be induced which is reversed on reversing the current.

Hörmann (l. c.) has already shown that the increased excitability at the kathode on making, and at the anode on breaking, the current constitutes an excitation when sufficiently strong currents are used, so that

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[1] Bot. Ztg., 1882, p. 257.
[2] Müller-Hettlingen, Pflüger's Archiv f. Physiol., 1883, Bd. XXXI, p. 212.
[3] For literature see Pfeffer, Pflanzenphysiologie, 2nd ed., Vol. XI, p. 122.
[4] Flora, 1873, p. 122.

a reversal of the current reverses the points at which the respective stimuli originate. It remains, however, to be seen whether prolonged weak currents exercise any analogous effects. As a matter of fact, a current weakened by the interposition of a resistance coil produces a much greater effect when it passes through the long axis of an elongated cell than when it traverses the cell transversely to its length, and to the direction of streaming. Since, however, the total resistance to the current is nearly the same in both cases, the same current traverses a greater length of the cell in the first case, and is also more concentrated in ampères per unit area. Hence the greater effect. If the current in the first case is restricted by means of vaseline insulations to as short a length as possible of the cell, approximately the same influence is produced as when it crosses the cell transversely. Similarly in cells which are approximately cubical, the effect produced by the current seems to have no relation to its direction with regard to the plane of rotation.

When a weak current has been acting for some time, irregular variations in the rapidity of streaming often take place, and recur at more or less regular intervals. Streaming may then be temporarily more active in one region of the endoplasm than in another (rapid successive observations), the change of *tempo* being rapidly propagated around the cell, leaving the entire endoplasm temporarily rotating more actively. Similarly when a period of retardation begins, the current may be at first slower on one side of the cell or on one side of the indifferent line, than on the other. These variations are usually shown in dying cells, and do not seem to have any connexion with the direction of the current which is causing them.

Similarly the kinetic inertia even of slowly streaming endoplasm is too great to allow a weak current in virtue of its (extremely feeble) electro-magnetic properties to exercise any directive influence upon floating paramagnetic or diamagnetic particles. A sudden shock or a strong current temporarily or permanently deranges the motor-mechanism, whereas prolonged weak currents influence the protoplasm as a whole, and streaming only secondarily, whether they produce an acceleration and subsequently a retardation, or retard streaming from the first.

CHAPTER IV

THEORETICAL AND GENERAL

SECTION 45. The supposed Analogy between the Shock-stoppage of Streaming and a Muscular Contraction.

HÖRMANN (l. c.) considers that the shock-stoppage of streaming corresponds to an ordinary muscular contraction, and that the different response is due to the different structure of the motor-mechanisms in the two cases. In support of this conclusion he points out that a similar current of action (negative variation) accompanies an excitation, and is often entirely restricted to the latent period preceding the response, as it always is in a stimulated striated muscle. This negative variation is, however, simply a special instance of the general law enunciated by Hermann [1], that an excited or injured area in a continuous mass of protoplasm always becomes electrically negative to the uninjured or unexcited portions. Hence the duration of the negative variation at any point corresponds to the length of time the protoplasm remains excited, and if the stimulus is propagated so also will be the negative variation.

The amount of work done by a contracting muscle represents a very large portion, often as much as one-fourth, of the energy of the food consumed, but the work done by the streaming plasma in plant-cells represents only a very small fraction of the energy of respiration. Moreover, the plasma of a quiescent muscle is at rest, but probably moves on contraction, and rearranges itself within a framework of elastic tubes, whose elasticity forms a prominent factor in the contraction and subsequent relaxation.

Another essential difference is that the liberation of energy and production of heat increases in the contracting muscle, but either remains the same or decreases when rotation ceases. The latter is an instance of inhibition, comparable in a wide sense to the stoppage of the heart's beat produced by the action of certain stimuli upon the inhibitory nervous mechanism. This analogy affords no proof of the existence of any such mechanism in plant-cells, and it is even doubtful whether any special conducting organs normally exist in the form of protoplasmic

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[1] Handb. d. Physiol., Bd. I, Th. I, p. 224.

fibrillae, which in streaming cells would necessarily be confined to the non-moving layer of ectoplasm.

SECTION 46. **Nerve-fibrillae in Plants.**

Němec[1] states that longitudinal strands of fibrillae can be seen in the cells at the apices of roots, and that these are always connected with the nuclei in young cells. These fibres seem to pass from cell to cell along the longitudinal rows of cells in the plerome, but when present in the periblem they are usually more radially arranged. They were observed by Němec only in dead cells fixed in acid media, or just before the death of cells placed in neutral or alkaline methyl-blue. Klemm[2] has, however, shown that fibrillar structures can be produced by the action of various chemical agents, and that this condition of the protoplasm is only temporary, if it be not fatally affected. Similar temporary but pronounced longitudinal striations were observed by the author[3] in plant-cells as the result of treatment with ether.

Němec (l. c., pp. 110 seq.), however, states that chloroform, ether, plasmolysis, low and high temperatures cause the fibrillar bundles observed by him to disappear[4]. He also finds that they become more strongly marked as the result of stimulation. Apparently, therefore, although not permanent structures, they may represent the channels along which stimuli are more readily transmitted than through the general protoplasm. If so, their increased development after stimulation would partly explain the slow but ultimate response of far removed parts to stimuli, which produce no effect upon them if of short duration.

According to Němec (l. c., p. 128), small but sudden changes of temperature cause the fibrillae to disappear, and the power of propagating stimuli is almost or entirely lost until they reappear again. This apparent connexion with the reappearance of the fibrillae may, however, be merely accidental, for the sudden change of temperature may have temporarily inhibited the power of response, and not the power of propagation. In any case, the rates of propagation given by Němec are slower than in certain cases observed by the author in which no fibrillar bundles were perceptible.

Comparison between a nerve-muscle preparation and a streaming cell. Hörmann apparently supposes a close analogy to exist between a nerve-muscle preparation and a *Nitella* cell, but a variety of facts

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[1] Die Reizleitung, Jena, 1901, p. 71.
[2] Jahrb. f. wiss. Bot., 1895, Bd. XXVIII, p. 696.
[3] Ewart, Journ. Linn. Soc., 1895, Vol. XXXI, p. 411.
[4] Similar effects were noted in the rudimentary nerve-fibrillae of animals by Monckenburg and Bethe, Archiv f. mikr. Anat., 1899, Bd. LIV.

negative this assumption. Thus dilute glycerine excites contractions when it comes into contact with the nerve or nerve-ending of a nerve-muscle preparation, but not if the latter is curarized, whereas if applied to a *Nitella* or *Chara* cell, which has recovered from the first shock-stoppage due to the action of a dilute solution of curare, dilute glycerine usually accelerates streaming, while dilute salt solution always retards it, although a crystal of salt readily excites the nerve of a fresh nerve-muscle preparation and produces a muscular contraction. Similarly an electrical stimulus produces the same shock-stoppage in a curarized cell as in the absence of curare, the only difference being that the latent period of recovery is slightly prolonged. On the other hand, in a curarized nerve-muscle preparation the motor end-plates are paralysed, and the muscle responds to direct excitation, but not to stimuli applied to the nerve.

Similarly veratrin, muscarin, atropin, &c., are powerful neuro-muscular poisons, the first two acting almost entirely on muscle alone, but they exercise a relatively feeble action on streaming plant-cells. Apparently, therefore, the latter do not possess anything corresponding even approximately to the neuro-muscular mechanism of Coelomate animals, and if there is any differentiation into better-conducting fibrils and feebly conducting ground substance, it must necessarily be of very rudimentary character, and is probably for the most part only a temporary development.

SECTION 47. Transmission of Stimuli and rate of Propagation in Cells and in Tissues.

Stimuli are probably transmitted both longitudinally and transversely through the ectoplasm and endoplasm, just as they are in a muscle-fibre. In a striated muscle-fibre the stimulus is rapidly propagated (1 to 13 mm. per second), whereas in cells of *Nitella* and of *Chara* the rate of propagation at room-temperature appears to lie between 1 and 8 mm. per second, which is less rapid than that in the muscle of the heart (10 to 15 mm. per second). This rate of propagation is, however, sufficient to show that the streaming plasma (1 to 3 mm. per minute), is not responsible for the transmission of stimuli. More exact determinations than the above are difficult, even when very long cells of *Chara* or *Nitella* are used. This is chiefly owing to the variable duration of the latent period, which necessitates rapid successive observations of the time of stimulation and of stoppage at the stimulated and unstimulated ends of the cell. The difference between the first two times gives the latent period of response, and on subtracting this from the interval of time between the application of the stimulus and the stoppage at the unstimulated end, we get the time of propagation through a distance equal to the greater part of the length of the cell. Single induction shocks were applied to an end of the cell insulated by vaseline, and the times determined by the aid of

a metronome. In a few cases the rate of propagation was as much as 20 mm. per second at 18° C., which in short cells causes a practically simultaneous cessation over the entire cell.

Hörmann (l. c.) observed that an electrical stimulus applied to one end of a cell of *Nitella* progressively decreased as it travelled along the cell, in some cases becoming sub-minimal before reaching the other end. Apparently, therefore, the stimulus encounters considerable resistance in its passage through the protoplasm, and rapidly loses energy as it travels onwards. Stimuli cannot be increased beyond a certain intensity, for above this intensity the protoplasm is fatally affected. Hence a stimulus of limited duration, however intense, cannot be transmitted beyond a certain distance through undiffentiated protoplasm, and this distance is determined more by the conductivity of the protoplasm than by the character and intensity of the stimulus.

Transmission from cell to cell. Hörmann also concludes that inhibitory stimuli may be transmitted from one cell of *Nitella* to another by means of interprotoplasmic communications, though none have as yet been seen in this plant. In this respect an analogy would exist with involuntary muscle-tissue, through which stimuli are propagated from fibre to fibre in the absence of motor-nerves. The proof is, however, open to doubt. Electrical, thermal, and mechanical stimuli were used, and in all cases a powerful stimulus is necessary; the stoppage then occurring frequently almost simultaneously in the two cells. The author has never observed a propagation of locally applied thermal or electrical stimuli beyond the next axial cell, and hence the apparent transmission is probably due to lateral diffusion when an electrical stimulus is used, or when cold is applied, to its direct transmission through the dividing wall. The stimulus is never transmitted to the whorled leaves at the node, probably because of their relatively small points of attachment. Mechanical stimuli may travel through two or three cells, but this is simply because they are rapidly propagated in the form of a pressure wave through the cell-sap, and from cell to cell through the elastic end-walls on which this wave impinges.

As a matter of fact there appears to be no vital mechanism in plants for the *rapid* transmission of stimuli from cell to cell, but instead physical means such as hydrostatic disturbances are used. Stimuli may be vitally transmitted from cell to cell by interprotoplasmic communications, but the rate of propagation seems always to be slow, a time-block apparently occurring at each passage from cell to cell. Hence the rate of propagation is more rapid in rows of elongated cells, than in rows of short ones. For example: a stimulus exciting streaming is transmitted more rapidly along the midrib of a leaf of *Elodea* than through the cells of the lamina.

A temporary stimulus only produces a very localized effect, since it suffers a steady decrement in passing from cell to cell. If, however,

a stimulus such as contact, or the effect of injury, acts for a prolonged period of time, it may be transmitted for some distance (1 to 30 mm. or more) with but little diminished effect, the successive hindrances to its passage being apparently gradually overcome[1]. Thus the infliction of an injury upon a leaf of *Elodea* or *Vallisneria* causes a stimulus inducing streaming to pass slowly from cell to cell for some distance. By noting the interval of time between the commencement of streaming in cells at measured distances along the same longitudinal path, the average rate of propagation can be determined. The average rate of propagation along the midrib of *Elodea* varied from 1 to 2 mm. per minute at 18° C., and from 1·4 to 0·4 mm. per minute at 30° C. In the longer leaf-cells of *Vallisneria* the rates were 1·2 to 0·5 mm. per minute at 18° C., and 2 to 0·8 mm. per minute at 30° C.

In many plants when wounded, the neighbouring cells respond to the injury by a movement of the nucleus to the injured side, and an aggregation of the protoplasm on the same surface. Using this reaction as a test for the reception of the stimulus, Němec (l. c., p. 35) observed a maximal rate of propagation in root-apices of 0·3 mm. to 0·1 mm. per minute at room-temperature. This lower rate is probably partly due to the smaller size of the cells. Moreover, the intensity of the stimulus rapidly decreases at a certain distance from the injury, and since the time of reaction undergoes a corresponding increase, the actual rate of propagation is more rapid than it appears to be. Thus with observations commencing three minutes after an injury had been inflicted, a wound-stimulus travelled in the next two minutes 0·55 mm. (0·27 mm. per minute), and in the next seven minutes only 0·33 mm. (0·05 mm. per minute).

According to Němec (l. c., p. 49), the rate of propagation is not influenced by light. As regards temperature, no reaction occurs at 2° C.; at 6° C. a slight reaction is shown after a quarter of an hour for a distance of 0·2 to 0·9 mm.; at 9° C. the reaction is nearly as rapid as at 18° to 20° C.; at 42° C. the apparent rate of propagation is nearly the same as at 6° C., and at 35° C. about the same as at 9° C.; at 43° C. no reaction being shown. The time of reaction and the actual rate of propagation are unfortunately not kept separate in these results, and hence they lose considerably in value.

SECTION 48. **Passive or Active Movements by the Chloroplastids.**

Chloroplastids floating in a stream of plasma can often be seen to rotate obliquely or horizontally on their own axes, or to roll over as they are carried onwards by the moving stream. Jurgensen and also Velten

[1] Cf. Ewart, Ann. du Jard. Bot. de Buitenzorg, 1898, Vol. XV, pp. 190 seq.

considered the rolling movement to be an active one, due to the chloroplastid itself[1]. It is, however, readily explained by the existence of irregularities on the inner surface of the ectoplasm, and by the fact that the velocity in the different layers of endoplasm is by no means precisely uniform. Frequently, however, two neighbouring chloroplastids may appear to be rotating on their axes in opposite directions, one against and the other with the hands of a watch. Berthold[2] considers this to be due to the chloroplastids being inclined in opposite directions to the observer as they roll against the ectoplasm. Seen from above this would give the appearance of rotating in opposite directions[3]. This explanation is borne out by the fact that a chloroplastid, while retaining the same inclination, may be seen to turn over and yet continue to rotate in the same direction as before, whereas if the movement were an active one, it should have been reversed. The latter does, however, actually occur in the chloroplastids of Characeae, according to Hörmann (l. c., pp. 30 seq.), who has also observed chloroplastids continue to rotate in a mass of plasma in which streaming had ceased. Similar observations which seemed to indicate an inherent power of movement in chloroplastids were first made by Dutrochet[4]. Chloroplastids lying on the indifferent line may rotate for a time without changing their position, but in every case observed by the writer there was always a possibility that the extreme edge of the chloroplastid was in contact with moving endoplasm, and the temporary adherence to a particular locus is in no wise contradictory to this explanation.

If the chloroplastids of Characeae have an active power of rotary movement of their own, then they differ in this respect from all other chloroplastids, for these are always passively carried by the streaming plasma. In *Elodea, Vallisneria*, &c., the dividing line between the moving and non-moving layers may move centrifugally outwards until the whole of the chloroplastids are in movement, and only a thin non-moving film remains in contact with the cell-wall. In *Chara* and *Nitella*, however, this never happens; the outer boundary of the moving layer maintaining a constant position within the chlorophyllous layer, and chloroplastids being relatively rarely drawn into it. Hörmann supposes that in passing through the limiting layer[5] the chloroplastid becomes covered by a special film of protoplasm which acts as a motor-mechanism, and endows the

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[1] Jurgensen, Studien d. Physiol. Inst. zu Breslau, 1861; Velten, Sitzungsb. d. K. Ak. d. Wiss., math. und nat. Klasse, 1876, Bd. LXXIII, I, p. 350; Flora, 1876, p. 85.

[2] Protoplasmamechanik, 1886.

[3] This can easily be demonstrated by rolling two blackleads inclined in opposite directions along a walking-stick, and viewing their upper ends.

[4] Ann. sci. nat., 1838, T. IX, ii. sér., p. 15.

[5] Hörmann regards this layer as the active seat of movement.

chloroplastid with a power of spontaneous movement. All these conclusions of Hörmann's are, however, practically based upon the single above-mentioned observation made upon a dying cell of *Nitella*, an observation, moreover, which the writer has been unable to repeat. Against it we have the following positive observations: (1) rotating chloroplastids exert no such counteraction upon neighbouring particles as might be expected if they possessed an active power of movement differing from that in the cytoplasm; (2) chloroplastids killed and bleached by sunlight may exhibit the same rotary movements as living ones, and it is highly improbable that a dead chloroplastid could maintain permanently attached to it the active layer of protoplasm that Hörmann postulates; (3) isolated chloroplastids never show any active translocatory movements, however long they may remain living under observation [1].

Velten (l. c.) observed that when the protoplasm was coming to rest, the chloroplastids often appeared to strike against the plasma, and concluded from this that all chloroplastids possess an active power of translocatory movement. Dutrochet (l. c., pp. 17, 73) even went so far as to regard the chloroplastids as the active agents in producing streaming movements in *Chara* and *Nitella*. Obviously Dutrochet was unaware of the existence of streaming in the non-chlorophyllous rhizoids of these plants. Velten's conclusion is decisively negatived by the fact that dead bleached chloroplastids may exhibit the same phenomenon as that observed by him. The peculiarity is probably due to one or more of the following factors: (1) the momentum of the chloroplastids, (2) local variations in the viscosity of the protoplasm, and hence unequally distributed internal friction, (3) local inequalities in the activity of the propulsive mechanism.

A closely allied question is whether the slow epistrophic and apostrophic movements of the chloroplastids due to the action of light are active or passive in character. In some cases, as for example in *Mesocarpus*, it has been tacitly assumed that the movement was active, although no direct proof has ever been brought forward. It is certainly suggestive that in motile unicellular organisms, the movements carried out under the action of light are performed by the entire organism, and not by the chlorophyllous part of it. Similarly in higher plants, it is the protoplasts as a whole which perceive and respond to light-stimuli. It is even doubtful whether the chloroplasts act as percipient organs for light at all.

According to Frank [2], however, the movements are passive, whereas Moore [3] considers them to be active. The latter author is, however, unable to adduce sufficiently satisfactory evidence in support of his view. Isolated

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[1] Cf. Ewart, Journ. Linn. Soc., 1896, Vol. XXXI, pp. 423–7.
[2] Bot. Ztg., 1872; Jahrb. f. wiss. Bot., 1872, Bd. VIII.
[3] Journ. Linn. Soc., 1888, Vol. XXIV, p. 240.

chloroplastids of *Vallisneria, Elodea, Lemna*, Fern prothalli, &c., though they may remain living and capable of CO_2-assimilation for several hours, never show any directive movements in response to light however intense, however they may be placed, and in whatever media they may be immersed. Hence, apparently, the chloroplastid can only move when imbedded in living plasma, and whether the movement is due to a reaction between the two or is due to the cytoplasm alone, still remains an open question.

SECTION 49. **Theories of Streaming.**

Brücke and also Hanstein [1] have suggested that the moving protoplasm circulates in closed tubes, which are either themselves at rest, or which rhythmically dilate and contract. This is, however, highly improbable and devoid of proof either by experiment or observation. The mere fact that relatively large chloroplastids commonly swim in the stream when the movement is active, would necessarily postulate tubes of corresponding width, whose walls would be easily distinguishable if they possessed the necessary physical and vital properties. It is indeed sufficient to follow a floating chloroplastid a few times round a cell to convince one's self of the impossibility of the existence of any such tubes. The theory that streaming is a phenomenon of contractility is no longer tenable, since it postulates the existence of a fixed contractile framework, or of firm elastic boundaries to the moving streams. Frequently the indifferent line between two opposed streams has no perceptible breadth. Yet the streams do not interfere or commingle in the least and behave as if separated by a stationary invisible membrane. This may be a surface-tension film of oily or other substance which possibly is not wetted by either stream, and which possesses sufficient elasticity to repel slowly moving solid particles which collide obliquely against it.

Hofmeister and Sachs [2] have suggested that changes in the power of imbibition of the protoplasmic particles might cause some to temporarily extrude water, others to absorb it. Waves of such action and reaction passing around the cell would cause the protoplasm to move in a particular direction. The free water of the protoplasm must, however, move in the opposite direction with a velocity corresponding to the relative masses of it and of the protoplasm. This mode of propulsion involves a very high internal friction, and a correspondingly large consumption of energy, whereas the actual consumption of energy has been shown to be relatively small (Sect. 10). Moreover, the rhythmic imbibitory changes which should

[1] Brücke, Unters. über das Protoplasma und die Contractilität; Hanstein, Protoplasma, Heidelberg, 1880.

[2] Hofmeister, Die Lehre von der Pflanzenzelle, p. 63; Sachs, Physiologie, 1865, p. 451.

theoretically counterbalance and involve no external consumption of energy, would not do so in practice, for the protoplast is far from being a perfect machine, and indeed is in many respects further from perfection than a steam-engine.

If cells of *Trianea*, *Elodea*, *Vallisneria*, &c., are placed in localized contact with a drop of a fairly strong solution of methyl-violet or cyanin [1], it can often be seen when streaming is very slow that the dye is carried with the plasma and not in the opposite direction (Fig. 13). Hence we may safely conclude that the protoplasm and the contained free water move in the same direction.

If the water were absorbed from and excreted into the cell-sap in such a manner as to produce forward movement in the protoplasm, the cell-sap would of necessity rotate in the opposite direction to the protoplasm, and with greater velocity than it. Neither of these conditions, however, ever occurs in plant-cells. An oblique *external* exudation of water is impossible in the case of cuticularized hair-cells which exhibit streaming, and as regards uncuticularized cells immersed in water, a simple calculation shows that a cell of *Nitella* exhibiting active streaming would need to absorb and excrete more than 2000 times its own volume of water in the course of a day. Suspended particles in the immediate neighbourhood of the cell exhibit no signs of any such exudation, which moreover the physical properties of the cell-wall render impossible.

It is also certain that the motion is not produced in a similar manner to the phenomenon of thermo-diffusion, for the necessary difference of temperature does not exist, and the other conditions are not fulfilled.

There only remain to be discussed the electrical theories put forward by Amici, Dutrochet, and Velten, and the surface-tension theory as propounded by Berthold, none of which, however, affords a completely satisfactory explanation.

SECTION 50. **Electrical and Electro-magnetic Theories of Streaming.**

Amici [2] concluded that the chloroplasts acted as Voltaic elements, and electrically propelled the endoplasm. This theory was accepted by Dutrochet and Becquerel, but is now no longer tenable, even although Velten and Hörmann (l. c.) still consider the chloroplastids to have an independent power of movement of their own. One experiment performed by Becquerel was to pass a current through a spiral wire arranged parallel

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[1] Solutions which rapidly tinge the protoplasm must be used, although these shortly prove fatal. Cf. Pfeffer, Unters. a. d. Bot. Inst. zu Tübingen, 1886, Bd. II, p. 201.

[2] Cf. Dutrochet, Ann. sci. nat., 1838, ii. sér., T. IX, p. 78; also Dutrochet and Becquerel, l. c., pp. 85–7.

to the lines of streaming, but neither at make nor break could he observe any change in the velocity of streaming. The negative results were simply due to the fact that the induced currents were too weak and of too short duration to produce any perceptible effect, but they led Becquerel to conclude that the electromotive mechanism must be of very special character.

Velten [1] was able in dead cells, by using strong constant currents, to cause more or less regular streaming motion of small particles of disorganized protoplasm around the cell, and the direction of movement was reversed on reversing the current. Bearing in mind the magnetic

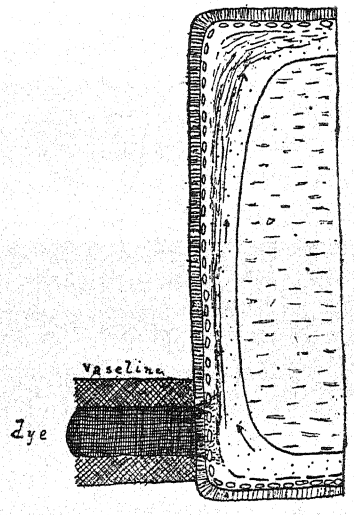

FIG. 13. Diagram of half of young *Chara* cell with locally applied dye.

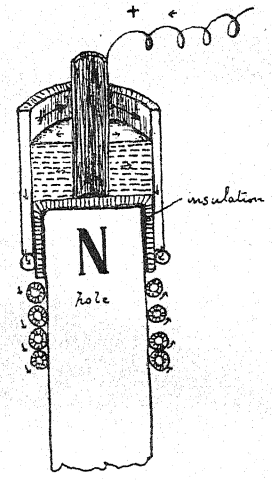

FIG. 14. Sectional diagram of electro-magnetic streaming. The small arrows show the direction of the electrical current and the large ones the movement of the mercury.

properties of the cellulose membrane, it seems very probable that this is an electro-magnetic phenomenon, but in any case no such reversal of the direction of streaming can be produced in living cells by the direct action of electrical currents. It is true that as the result of the injury and death of neighbouring cells the direction of streaming may after a period of quiescence be opposed to the previous one; but this is an exceedingly rare phenomenon, and is probably the result of some complicated secondary reaction.

That weak electrical currents continually circulate in living plant-cells is certain, for at the outer and inner surfaces of the protoplasm, dissimilar solids wetted by dissimilar saline solutions are in contact, and

[1] Bot. Ztg., 1872, p. 147; Flora, 1873, p. 82.

hence the electrical potentials of the two surfaces also[1] differ. The unceasing chemical action in the protoplasm can easily therefore maintain currents circulating from one surface to the other according to the local differences of potential and of conductivity.

The theory that streaming is due to the repelling action of opposed currents in ectoplasm and endoplasm necessitates the highly improbable assumption of the existence of an insulating layer between them, and is moreover contradicted by the fact that when streaming becomes very active in *Elodea*, *Vallisneria*, only the merest film of ectoplasm may remain adherent to the cell-wall. Hence it is useless to discuss what the direction of these currents would need to be in regard to that of streaming.

A greater degree of probability attaches to what may be termed the electro-magnetic theory, which necessitates the assumption of either a permanent polarity in the magnetic cellulose membrane or a temporary one induced by the action of electric currents. A simple mode of showing the production of motion in a fluid by electro-magnetic action, is to place a box with a glass bottom on one pole of an electro-magnet and to pass an electric current through the mercury and round the magnet as shown in Fig. 14. The same current causes the mercury to move, and induces strong polarity in the magnet. Similarly, the passage of a current through the endoplasm at right angles to the direction of streaming would suffice to produce and maintain movement in a particular direction. The existence of such a current would necessitate a reverse one to complete the circuit. This might take place inwardly or outwardly along the indifferent line, and since the current would be in a closed internal circuit, it would be difficult or impossible to detect without fatally injuring the cell. Moreover, if the cell-membrane was a magnetic shell with its inner and outer surface as poles, it would not exhibit any perceptible polarity. This mode of propulsion, however, involves a corresponding backward reaction upon the cell-wall, just as the magnet in Fig. 14 tends to revolve in the opposite direction to the rotating mercury. We have already seen that it is highly doubtful whether any such backward reaction is permanently exercised upon the outer layers of the cell by the streaming endoplasm.

It does not necessarily follow that an electric current passing longitudinally through a cell should retard streaming in one direction and accelerate it in the other, for the current is at right angles to the supposed action current, and hence may not affect the propulsive mechanism. When currents are passed through at right angles to the direction of streaming, the latter is occasionally accelerated or retarded more on one side than on the other, but this is more probably an electrolytic effect than the result

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[1] It is possible that the greatest difference of potential exists between the cell-wall and cell-sap, the protoplasm acting as the chemical medium separating them.

of summation with and antagonism to the action currents on the opposed sides of the cell.

The fatal objection to the theory is that streaming is not directly affected in a strong magnetic field however the cell may be placed. Moreover, streaming in protoplasmic threads is very difficult to explain on the above hypothesis, especially when, as in very fine threads, the streaming is all in one direction [1].

In very fine threads, however, the inwardly directed surface-tension becomes considerable relatively to their bulk, so that the threads behave like thin-walled elastic tubes, and a passive propulsion of the plasma through them by the pressure behind becomes possible.

SECTION 51. Surface-tension Theory.

This was first propounded by Berthold [2], who considers that all protoplasmic movements can be directly referred to simple physical causes, such as differences of surface-tension and the like. Thus he compares the movements of Amoebae and of swarm-spores with the movements of drops of oil in an emulsion, or of water or benzine in the presence of alcohol, or of a piece of camphor floating in water, the movement always occurring towards the side of least surface-tension. This latter statement is, however, misleading. In the case of a piece of camphor floating on water the surface-tension is lowered unequally as the camphor dissolves irregularly. The fragment is drawn to the side where the surface-tension of the water is greatest; for the surface-tension film moves in that direction, and drags the camphor after it. In the particles of an emulsion, however, a diminution of the centrally-directed surface-tension pressure on one side or an increase on the opposite face causes the particle to move to the side of least surface-tension, and this movement will continue as long as the potential difference is maintained, and will cease as soon as equilibrium is reached.

A direct physical explanation can, however, hardly apply to organisms which possess definite locomotory organs, such as flagellae or cilia. It is undoubtedly often the case that physical forces such as surface-tension, osmosis, imbibition, &c., when intense, may overpower the organism, but there can equally be no doubt that the latter has acquired the power of directing and controlling these natural forces for its own benefit, so that a simple direct physical explanation can hardly be postulated for phenomena which may be due to a multiplicity of interacting factors, viz. the attraction of swarm-spores by light, and their repulsion when the illumination is intense.

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[1] Cf. Velten, Flora, 1873, p. 98.

[2] Protoplasmamechanik, 1886, pp. 119 seq.

A satisfactory theory must conform to all the conditions existing within the cell. It appears that the peripheral layer of cell-sap is passively carried along by the vacuolar membrane, which it wets and to which it adheres. The rapidity with which this velocity decreases inwardly depends upon the friction between the successive layers of cell-sap, i. e. upon its viscosity. The energy of motion is derived directly or indirectly from the metabolism of the moving layers themselves, for by sudden plasmolysis it is sometimes possible to cause portions of endoplasm to separate and show streaming for a short time. Since under normal conditions the force or forces inducing movement do not appear to

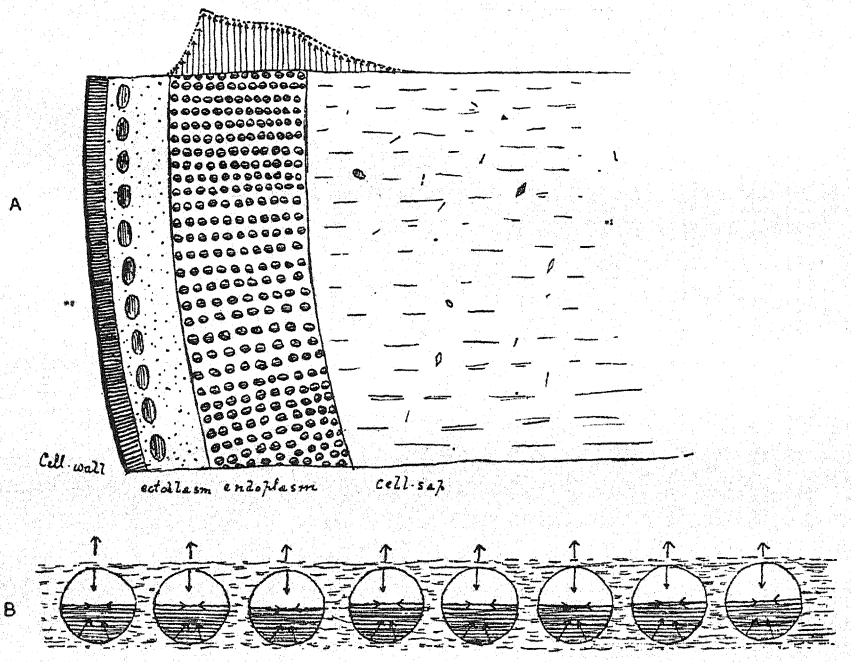

FIG. 15. A. Diagram of section of *Chara* cell, showing rows of emulsion globules in endoplasm. The row o arrows shows the relative velocities of different layers. B. Row of emulsion globules showing surface-tension forces and resultant movement.

exercise a corresponding reaction against either the ectoplasm or the cell-wall, the movement can hardly have an electro-magnetic origin, but probably belongs to the domain of molecular phenomena.

The activity of streaming depends upon the magnitude of the forces acting as compared with the resistance to be overcome. As was first shown by Nägeli (l. c.), slight localized streaming movements may occur in Desmids and other Conjugatae, as well as in the cells of many Phanerogams. The movement soon ceases and recommences elsewhere. Berthold (l. c.) has shown that similar movements occur in the interior of an emulsion

of Canada balsam with a solution of sulphur in carbon bisulphide, as the latter evaporates. It does not, however, follow that the cause of movement corresponds even approximately in the two cases, and, as a matter of fact, evaporation is impossible in Diatoms submerged in water, although diffusion or chemical action might play the same part in producing localized changes of surface-tension.

Berthold regards the regular rotation in vacuolated cells as being due to differences of surface-tension in the limiting layers of cell-sap and endoplasm, and considers irregular streaming to be of similar nature to the movements in emulsions. In the former case, since both protoplasm and cell-sap have each their own surface-tension films, being non-mixible fluids, streaming can only be induced by movements of the films transferred by friction to the neighbouring layers of protoplasm and cell-sap. It is not easy to see how continuous movement in a definite direction could be produced in this manner, for any localized increase of surface-tension would exert a centripetal attracting force upon all the surrounding regions of the film, and if the surface-tension were progressively increased around the cell, after a few rotations the breaking strain of the film would be reached, and a stoppage would ensue.

If, however, a series of rapid waves of increased surface-tension passed around the cell in a particular direction, this might induce a general movement of the film, and with it the protoplasm in a definite direction. Such differences of surface-tension might be produced by the inward and outward diffusion of dissolved substances, and hence would also affect the surface-tension film of the cell-sap. A surface-tension film of water against air can resist a maximum strain of 80 dynes per linear centimetre. Taking the force acting on a gramme of moving plasma as being from 10 to 200 dynes, a simple calculation showed that in the case of particular cells, of *Nitella*, *Chara*, and *Elodea*, the required strains upon the surface-tension films were always much below this limit. For example, in one case a gramme of plasma represented an internal surface of 42 sq. cms., which required a strain of from 15 to 30 dynes per linear centimetre to give the required propulsive force. There is, therefore, no physical obstacle to this theory, but there is a very serious practical one.

The density of the cell-sap is somewhat less than that of the protoplasm, but on the other hand it has a very much lower viscosity. Hence the rapidity of movement in the outer layers of the cell-sap should be less than that of the inner layers of the protoplasm, since the 'slip' is greater in the former case. For the same reason the velocity should decrease more rapidly inwardly than that of the protoplasm does outwardly. This is actually the case, but on the other hand, the velocity of small floating particles in the endoplasm of *Chara* and *Nitella* can usually be seen to *increase* from within outwards until a maximum is reached at a

variable, but usually small distance, from the non-moving ectoplasm, beyond which point the decrease to *nil* is very rapid. This affords conclusive proof that the force inducing movement does not act at the boundary of the endoplasm and cell-sap, but throughout the whole substance of the former. By this distribution of velocity the friction between the successive layers is in most cases reduced to a minimum, for when a liquid flows under uniform pressure around a curved path, the outer layers must move more rapidly than the inner if tangential friction is to be avoided.

The inwardly directed pressure exerted by the surface-tension films on the outer surfaces of the cell-sap and ectoplasm, and on the inner surface of the endoplasm, is greatest per unit area at the corners of the cell, owing to the convex curvatures at these points, and least at the sides where the membranes are flat. The actual surface-tension in each film is, however, the same throughout, and therefore no special influence would be exerted on streaming at the angles of the cell. Even in small cells the pressure due to surface-tension is never more than a small fraction of an atmosphere, and hence no appreciable diminution of the internal osmotic pressure is produced by it. When, however, rectangular cells with rounded angles and with uniformly permeable walls are placed in weak homogeneous plasmolyzing solutions, retraction of the protoplast almost always occurs first at one or other of the angles of the cell, owing to the influence of the convexity of the surface-tension films at these points in increasing the inwardly directed pressure due to surface-tension.

SECTION 52. **Electro-chemical Surface-tension Theory.**

If the wire from the positive terminal of an electrical battery is connected with a drop of mercury lying in dilute sulphuric acid, on connecting the negative terminal with the acid the mercury moves away from the positive pole. By making and breaking the circuit the mercury can be caused to creep to and fro. This phenomenon was first observed by Ermann in 1809, and it is due to the production by electro-chemical action of a difference in the surface-tensions on the two sides of the drop of mercury, the latter moving towards the side of least surface-tension. It is this principle which is utilized in Lippmann's capillary electrometer, and a feeble current will cause a relatively large amount of movement. Hence the propulsive force for streaming movements could easily be generated in some more or less closely analogous manner, although the precise character of the mechanism is impossible to postulate.

If the lowering of surface-tension took place on the same side of all the particles in an emulsion, they would move in this direction, for the inwardly directed pressure due to the surface-tension on the other

side would exert a propelling force in the given direction, which would continue as long as the difference of surface-tension was maintained. If the particles were close together and the emulsion confined in a spherical vessel, a regular motion of rotation would be exhibited so long as these conditions were maintained (cf. Fig. 15).

Now in the typical cell we have the following factors (1) a magnetic membrane, cellulose, surrounding (2) a double layer of a protoplasmic emulsion containing paramagnetic (albumin, chlorophyll, iron salts, &c.), and diamagnetic substances (water, starch, various proteids, oil, salts, &c.); (3) the outer and inner surfaces of this layer are at different potentials, since they touch different substances and saline solutions; (4) continuous chemical action goes on in the layer. We have therefore all the conditions for the production of inwardly or outwardly directed electrical currents, and for the maintenance of a directive action on floating particles composed of dissimilar materials. Suppose that the surface-tension of the ends pointing in a given direction always decreases when an electric current traverses the particles, then the emulsion as a whole will move in this direction, provided that the particles affected are close together and the viscosity of the emulsion not too great.

The presence of a cell-wall does not form an essential factor for the existence of regular streaming movements, but an organized arrangement of the protoplasmic particles is equally possible in its absence. Streaming in threads presents some difficulties, for the surface of the thread being bathed all round by cell-sap will be practically equi-potential (electrically) at all points. It is, however, possible that electrical currents might traverse the thread longitudinally. Moreover, since the surface-tension pressure is considerable in thin threads, passive propulsion by pressure from behind is possible through them, just as though they were very thin-walled tubes. In this case the streaming would be most active in the centre of the thread, or in the deeper layers if two opposed currents are present. On the other hand if streaming in protoplasmic threads is due to movements of the surface-tension films, then it would be most active in the outer layers. Unfortunately it has not been found possible to determine the existence of any *constant* difference of velocity between the outer and inner layers, even when the most minute floating particles are used as indicators. Differences of velocity are often shown, but without any apparent common origin; and in fact in thick threads a portion may be at rest or nearly so.

In any case, the detailed behaviour of streaming cells in response to weak (acceleration) and strong (stoppage or retardation) electrical stimulation lends support to the view that electrical currents are in part concerned in the production of streaming movements. The proof is, however, by no means so certain as Hörmann supposes (l. c., pp. 72 seq.), for precisely

similar evidence would lead us to conclude that glycerine and alcohol were also co-operative factors.

The shock-stoppage produced by so many agencies when suddenly applied may be the result of a temporary disturbance of the organized arrangement of the protoplasmic particles, supposed on the above hypothesis to be necessary for streaming. Mechanical stimuli, for example, might readily exercise some such action, although we might expect to find in this case, not a complete stoppage but irregular streaming in various directions for a time. The stoppage might also be due to sudden changes of surface-tension, produced first in the outer layers of protoplasm. The effect of these would be to give the protoplasm a tendency to move bodily inwards or outwards as the case might be. The former movement is prevented by the internal osmotic pressure, the latter by the cell-wall; but the effect would be to exercise a temporary drag upon the protoplasmic particles, which might be sufficient to arrest their movement.

These are, however, merely theoretical suggestions which may serve to stimulate inquiry, or which may afford a framework of hypothesis on which to hang facts. It is a fundamental error to suppose, as Hofmeister (l. c., p. 63) and Engelmann (l. c., p. 373) have done, that all protoplasmic movement must be produced in the same manner, that is by the interaction of precisely similar forms of energy with the same motor-mechanism. Even in the same cell the movement of a pulsating vacuole may have a different physical origin to that of streaming in neighbouring parts. Similarly the physical conditions in protoplasmic threads crossing the cell-sap are not the same as in the layers of protoplasm pressed against the cell-wall. It is true that transitions occur from sliding movements to circulation, and from circulation to rotation; but it is equally possible that more than one form of energy may be concerned, and that the motor-mechanism may include factors essential at certain times or in certain cases but not in all.

Just as all engines are not alike, nor are they all driven by steam, so also do different protoplasts differ in their internal constitution, and hence also in the manner in which they can utilize different forms of energy. Thus temporary localized sliding movements might easily be due to localized differences of surface-tension produced by irregular diffusion or by chemical action. Such movements might ultimately be aided or overpowered by those produced by the continuous interaction of electrical and surface-tension energy, and so regular streaming or rotation be produced.

Whatever the mechanism may be, the living organism exercises a certain controlling influence upon it: hence it does not necessarily follow that a chemical or physical agency will produce the same effect within a living cell that it does outside it. Moreover, a stimulus which retards streaming

in certain cases or under certain conditions may accelerate it in others. Not only may the viscosity of the protoplasm or cell-sap, and hence also the resistance to be overcome, vary, but in addition the relative amount of energy expended in streaming may alter within certain limits. Very probably also the manner in which the energy is utilized is liable to modification; and important changes must occur when the protoplast separates into streaming fragments, some of which may contain endoplasm only, or when the direction of streaming is altered, reversed, or undergoes a permanent local retardation. For all these reasons it is impossible to define precisely the conditions which a permanent theory of streaming must fulfil, and it must also take into account the possibility that the movement may not always be produced in an exactly similar manner.

Assuming that streaming in plants is the result of surface-tension forces, it is interesting to notice that animal physiologists incline to refer muscular contraction to the same natural agency. Thus [1], according to Bernstein, muscular contraction is the result of changes of surface-tension produced by chemical action. The changes of surface-tension are supposed to take place in the limiting layers between the walls of the fibrillae and the enclosed sarcoplasm, the effect being to cause the fibrillae to become shorter and broader. Possibly also an increase in the surface-tension of the sarcoplasm tends to make the cylindrical tubes into which it is broken up assume a slightly more globoidal shape. The purpose of the subdivision of the muscle-fibre into fibrillae is to increase the total surface at which surface-tension forces are active. Even then, however, surface-tension forces amounting to 0·304 gram per centimetre would be required to produce the maximal total force of contraction of which a frog's muscle is capable. The maximal force which a surface-tension film between mercury and water can exert is 0·42 gram per cm., and between olive oil and water is 0·021 gram per cm., and is probably even lower than this in the case of the media existing in the muscle-fibre. Hence Bernstein assumes that the fibrillae are broken up into still smaller units, of a probable radius of 10^{-5} cm. The resistance to rapid flow of a viscous liquid in tubes of this radius would be enormously great, and indeed it is doubtful whether the highest surface-tension forces would be sufficiently powerful to produce such flow. The theory does not, however, necessarily involve any flow in mass of plasma into and out of the tubes, or even from one part of the tube to another, since both the fibrillar walls and the enclosed sarcoplasm might have the same tendency to shorten and broaden.

There are, however, fundamental differences between the phenomenon of contractility as exhibited by a muscle-fibre and that of protoplasmic streaming as exhibited in plant-cells covered by a cell-wall or in undiffer-

[1] Naturwiss. Rundschau, 1901, Bd. XVI, Nos. 33–5.

entiated gymnoplasts. Even although the same natural forces are ultimately responsible for the movement in both cases, their origin, mode of application, and also the intrinsic character of the mechanism itself may differ widely. The dogma that all protoplasmic movement must necessarily be produced in a similar manner has even less justification than the older one which caused the existence of anaerobic organisms to be denied for a time. It is, indeed, doubtful whether any streaming movements in mass of the plasma of a muscle-fibre do actually occur, and the small size of most animal cells militates against the existence in them of any active internal currents in mass. The muscle-fibre has become specially differentiated for the performance of external work by external change of shape, but in the case of a streaming plant-cell no such active external change of shape is possible, and the work done is entirely internal. In the first case, the work done is intermittent and partly performed against the elasticity of the fibrillar net-work, whereas in the plant-cell the work is continuous normally, and is done against friction only. Moreover, it is by no means contrary to the theory of Natural Selection to suppose that these two forms of protoplasmic movement may possibly have arisen independently, just as various modes of locomotion have been independently acquired by different groups of plants and animals. This might still be the case even although in both cases the same form of energy was utilized for the production of movement. The wings of insects, birds, and bats afford, for example, instances of mechanisms of similar function, but dissimilar origin and structure, all three of which are driven by similar muscular energy and act against the resistance of the same medium.

It may, therefore, well be impossible to formulate any one theory which shall apply to all the known forms of protoplasmic movement, and it is extremely unsafe to make broad generalizations from data which may be really of limited and special application, or to attempt from observations made upon animal cells to deduce the conditions for protoplasmic movement in plants.

Summary of Results.

The energy of movement is generated in the moving layers themselves, and these are retarded by friction against the non-moving ectoplasm, and to a much less extent by friction against the cell-sap which is passively carried with the stream.

The motor-mechanism is such that no backward reaction is produced on the external or internal layers.

The velocity of streaming is largely dependent upon the viscosity of the protoplasm, and hence also upon the percentage of water in the latter, but the osmotic pressure exercises little or no direct influence upon streaming.

The activity of diosmosis is not necessarily increased by the existence of streaming, but secondarily induced differences of osmotic pressure may be perceptible between streaming and quiescent cells.

Albuminous solutions containing 89 to 90 per cent. of water have at 18° to 20° C. a viscosity of from 0·06 to 0·07 with 95 per cent. of water, 0·04 with 72 per cent., 0·29 C. G. S. units.

Gravity exercises little or no influence upon streaming in small cells, and only a very slight one on streaming in large ones. The velocity of floating particles of greater or less density than the plasma may be distinctly affected by gravity. This observation indicates that the viscosity of the streaming plasma is comparatively low.

As the temperature rises within certain limits the viscosity decreases, and a large part of the increased velocity of streaming is due to this cause alone.

To maintain velocities of 2 mm. and 0·4 mm. per minute in cells of 0·1 cm. and 0·01 cm. internal diameter, forces of approximately ·875 and 21·9 dynes respectively are required per gramme of moving liquid. The amount of work done in a year represents a consumption of only $\frac{1}{200000}$th of a gramme of cane sugar per gramme of moving liquid in the first case, and in the second represents only $\frac{1}{10000}$th of the energy of respiration, even if 99 per cent. of the energy intended for streaming is wasted. Hence the energy expended in streaming is a trifling fraction of that produced by respiration. The force required increases enormously as the diameter decreases, so that streaming or transference in mass of the highly viscous ectoplasm through interprotoplasmic connexions becomes practically impossible, although through the coarse pores of sieve-tubes a direct transference of the watery contents is possible[1].

The direction of streaming is mainly determined by internal factors, and in rotating cells a reversal is only possible in certain cases and under very special conditions. Changes occur spontaneously, however, in cells exhibiting circulation.

The total resistance during circulation is greater than during rotation, unless the velocity increases considerably, and hence a change from the former to the latter after stimulation is not due to an increased energy of streaming but to a change in the configuration of the protoplasm.

The energy for streaming can be derived either from aerobic or anaerobic metabolism. Certain species of *Chara* and *Nitella* are in fact

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[1] According to de Bary (Comp. Anat., 1884, p. 177) finger-like processes from the protoplasmic contents of adjacent segments of a sieve-tube meet in the sieve-pores but remain distinct. Flow in mass through the pores would involve the rupture of the limiting membrane, which would need a considerable pressure owing to the small diameter of the pores. This discontinuity has, however, only been observed in dead sieve-tubes. It probably results from the breaking of the viscous protoplasmic threads at their thinnest points on death, which is a surface-tension effect commonly produced in dying protoplasmic threads.

facultative anaerobes, and may exhibit slow streaming for six to eight weeks in the entire absence of free oxygen.

No special chemical changes are connected with streaming.

Of the different constituents of the cell, cellulose, albumin, and chlorophyll are paramagnetic, starch, sugar, oil, water, and probably myosin also are diamagnetic. Plant-cells usually, though not always, place their long axis parallel to the lines of force in a magnetic field.

The strongest magnetic field used exercised little or no direct effect on streaming, although a pronounced secondary effect is produced on prolonged exposure as the result of inductive action.

The connexion between certain forms of streaming movement and metabolism is a wholly indirect one, but this can hardly be a general rule.

Indirect relationships exist between streaming, growth, and assimilation, but no direct ones. Similarly the nucleus exercises no direct but a pronounced indirect influence on streaming.

An organized arrangement of the protoplasmic particles is probably an essential condition for regular continuous streaming. A great variety of agencies when suddenly applied seem to disturb this arrangement momentarily, and hence produce a temporary cessation of streaming. This shock-effect results from sudden changes of concentration, rapid falls or rises of temperature, momentary electrical excitation, and the sudden application of various poisons.

The minimal, optimal, and maximal temperatures for streaming vary according to the plant or cell examined, and also depend upon (1) the age or condition; (2) the external medium; (3) the duration of the exposure; (4) the supply of oxygen; (5) the rapidity with which the temperature is raised or lowered.

At temperatures above 30° C. the velocity immediately assumed is, in the absence of a shock-effect, always greater than that shown a few hours or a few minutes afterwards. Between 10° C. and 30° C. the permanent velocity is immediately or almost immediately assumed. Below 10° C. the acceleration due to a rise of temperature frequently does not become fully manifest until after a certain lapse of time.

In the case of facultative anaerobes, the response to changes of temperature is less pronounced in the absence of oxygen than in its presence. With short exposures, the optimum and maximum points are raised, but with prolonged ones the maximum point is lowered by the absence of oxygen.

Strong light retards streaming, while weak light may indirectly accelerate it in chlorophyllous cells. It is still doubtful whether streaming is affected by directly impinging electro-magnetic wave vibrations other than those of light. Mechanical disturbances may act as inhibitory stimuli, and may be propagated internally in the form of pressure waves.

Food-materials exercise both a direct and an indirect effect upon streaming. Acids, alkalies, and metallic poisons all retard streaming, and may cause a temporary shock-stoppage when suddenly applied.

Alcohols and anaesthetics when dilute may accelerate streaming, but when more concentrated always retard it.

Alkaloids which are strong nerve- or muscle-poisons have relatively little action upon the streaming cells of plants.

Weak electrical currents may accelerate streaming, strong ones always retard it, sudden shocks produce temporary cessation. The latent period of recovery decreases as the temperature rises up to a certain limit. Beyond this it increases. Weak constant currents lower the optimal and maximal temperatures for streaming.

A shock-stoppage is more readily produced by electrical stimuli at moderately high temperatures than at very low or very high ones, and in general the cells are more sensitive in the former case.

The electrical conductivity of the protoplasm undergoes a slight temporary increase on death, and it differs in the living cell from that of the cell-sap and cell-wall. The nucleus is fatally affected by electrical currents before the cytoplasm.

The effect produced by a weak constant current is not influenced by its direction with regard to the plane of streaming.

There is little or no analogy between a shock-stoppage of streaming and a muscular contraction, or between a nerve-muscle preparation and a streaming cell. No permanently differentiated nervous mechanism exists in plants, although temporary better-conducting channels may appear as the result of prolonged stimulation, or at certain stages in the development of growing organs.

Stimuli may be transmitted in the protoplasm of a cell of *Chara* or *Nitella*, at from 1 to 8 or even 20 mm. a second (18° C.), but the rate of propagation from cell to cell in tissues varies from 0·1 to 2 mm. per minute at 18° C.

The chloroplastids have no active power of movement of their own, but are passively carried with the moving stream.

The only kind of energy which appears capable of producing streaming movements under the conditions existing in plant-cells is surface-tension energy, and this is probably brought into play by the action of electric currents traversing the moving layers, and maintained by chemical action in the substance of the protoplasm. These currents may be supposed to act upon regularly-arranged bipolar particles of protoplasm in such a manner as always to lower the surface-tension on the anterior faces, and raise it on the posterior ones.

APPENDIX ON THE ELECTRICAL CONDUCTIVITY OF EGG-ALBUMIN[1]

ALTHOUGH it is not possible to obtain exact measurements of the electrical conductivity of protoplasm, it in all probability does not differ widely from that of such colloidal substances as egg-albumin containing corresponding percentages of water. It is also of interest to determine whether the decreased resistance following the death of the protoplasm is also shown when egg-albumin coagulates.

Using a battery of two standard cells it was at once seen that electrolytic decomposition occurred; bubbles of gas appearing on the electrodes, and the neighbourhood of the kathode becoming alkaline, and that of the anode acid. The resistance offered by an electrolyte depends in part upon the back electromotive force generated by the electrolytic products. In this case a voltameter, thrown into circuit by a key breaking the main current at the same instant, registered a maximum temporary deflection of 0·6 volt. The difference of potential due to the electrolysis is probably even higher than this, for a cell of 1·4 volts gave an extremely feeble current through two centimetre cubes of egg-albumin.

To obtain the true resistance the differential method must be employed, by using the apparatus shown in Fig. 16, in which the current can either be sent from the second to the third or from the first to the third electrode, that is, through a measured additional length of egg-albumin. The increase in the resistance gives the amount due to this additional length apart from any polarization effect. After each observation it is advisable to join up the electrodes for a short time, and then take an additional one with the current reversed. The resistance is most conveniently measured by the interpolation of known values in place of the egg-albumin, until the sensitive needle galvanometer used gives the same deflection. In addition, it need only be remarked that platinum electrodes must be used, and that these should be in the form of circular transverse plates which just fit into the tube, and are preferably insulated on the connected side.

Working in this manner values were obtained for the absolute resistance

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[1] This appendix was written after the foregoing paper had been read to the Royal Society.

of various samples of egg-albumin containing from 89 to 90 per cent. of water of from 340 to 400 ohms per cubic centimetre at 20° C. to 15° C. Within the range of temperature given, the source of the sample of albumin affects the conductivity more than the temperature does. A sample from

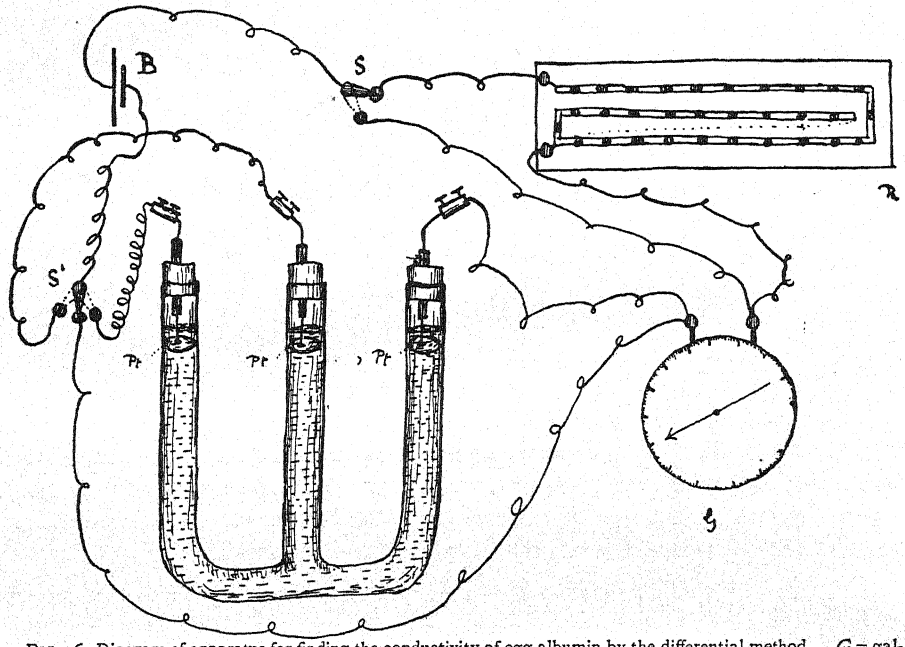


FIG. 16. Diagram of apparatus for finding the conductivity of egg-albumin by the differential method. *G* = galvanometer; *S*, *S'* = switch-keys; *R* = resistance-box; *B* = battery; *Pt* = platinum-electrodes, insulated on back and on wire with shellac.

a new-laid egg, for example, had a lower conductivity at 20° C. than that from an older one at 15° C., although in all cases the conductivity of the same sample of egg-albumin increases as the temperature rises. This applies even when the temperatures are such as to produce coagulation; and, in fact, the conductivity may be two-and-a-half times as great at 85° C. as it is at 18° C.

In illustration of this, the results of the following two experiments are appended:—

	Temperature.	Resistance in ohms per c. c.
A. Egg-albumin containing 89 per cent. of water.	18° C.	416
Coagulated at 90° C. and cooled to	85°	188
" " " "	18°	416
B. Egg-albumin containing 90 per cent. of water.	16°	501
Coagulated at 85° C. and cooled to	80°	235
" " " "	40°	400
" " " "	20°	485
" " " "	15°	510

These experiments were performed with the apparatus shown in Fig. 17, which was used on account of the difficulty otherwise experienced of removing the coagulated albumin from curved tubes. The resistances here include the polarization effect, and hence are higher than they should be; but an experiment performed by the differential method also showed that the conductivity of egg-albumin is unchanged by coagulation.

Egg-albumin containing water therefore conducts like a feebly saline electrolytic fluid, and has a correspondingly high resistance. We may safely conclude that the same applies to living protoplasm, in which also

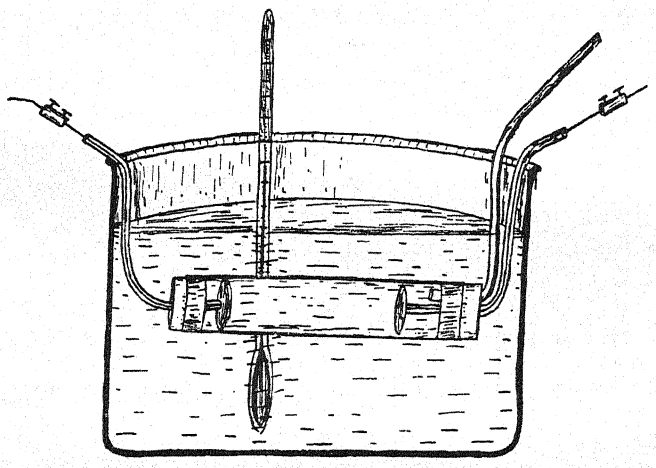


FIG. 17. Portion of apparatus for finding influence of temperature and of coagulation upon the conductivity of egg-albumin.

therefore the electrical resistance is partly dependent upon the velocity of the charged ions, which again is dependent upon the viscosity of the medium, water, through which they travel. The viscosity of water decreases with rise of temperature, and hence the velocity of the ions increases. A large portion of the increased conductivity is due to this cause alone.

The coagulation of the albumin is, however, without effect upon the viscosity of the water filling the intermicellar interstices of the coagulum, and hence is also without effect upon its conductivity. It is evident, therefore, that the mere coagulation of the dying protoplasm will not explain its slightly increased conductivity, which is in fact probably due to the liberation from it of electrolytic salts in the act of death—these being present in living protoplasm in smaller amount in the free condition. The same explanation possibly also applies to the fact that the conductivity of stale egg-albumin is somewhat greater than that of fresh samples, even although the percentage of water is the same in the two cases.

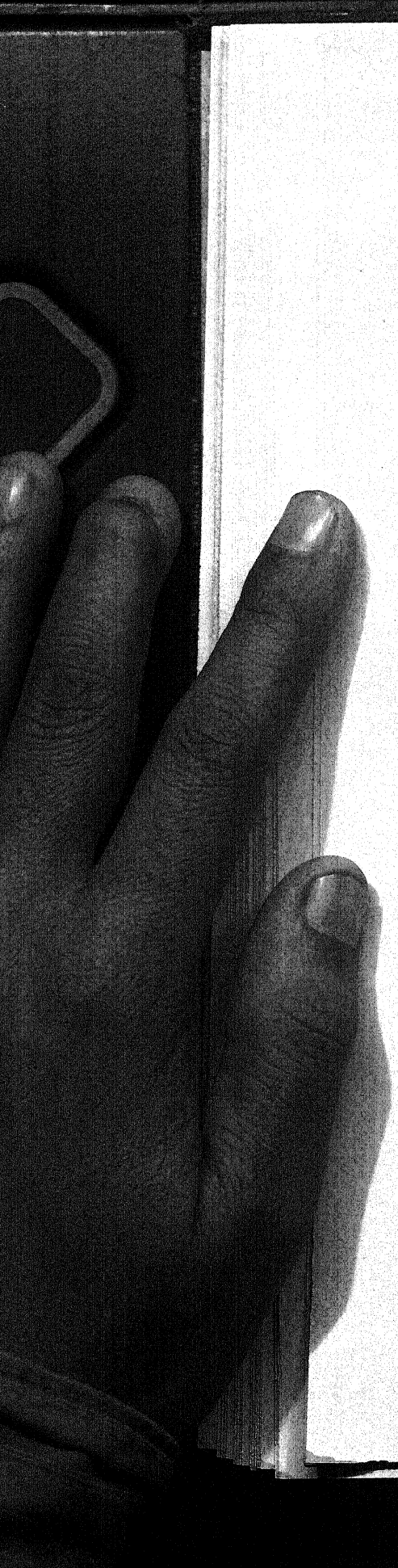
A thread of egg-albumin of 1 cm. in length and ·01 cm. diameter (·0000785 sq. cm. sectional area), would offer a resistance of nearly

500,000 ohms, so that a cell of 2 volts would send only ·000,000,4 of an ampère through it. A cell of *Chara* of about the same length and of less diameter than this allows considerably more current to flow through it, as indicated by the increased deflection of the galvanometer. From this it follows that either living protoplasm is a better conductor than egg-albumin, or more probably that the cell-sap and moist cell-wall have a higher conductivity than either protoplasm or egg-albumin.

In any case the resistance offered by protoplasm to the passage of an electric current is partly due to the electrolytic reaction, and is dependent upon the quantity and quality of the electrolytic salts in solution, decreasing to a certain extent with increasing concentration. The fact that previous electrical excitation may render a weaker current capable of stopping streaming may be merely the result of an increased conductivity of the protoplasm, produced by the liberation of electrolytic salts, allowing more current to pass, and hence increasing the shock-effect. Since, however, the same effect may be produced when single currents of extremely short duration are used, it seems more probable that it is actually partly due to an increased excitability of the protoplasm produced by the previous sub-maximal stimulation.

INDEX

THE END



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